

On Antarctic Entoprocta: Nematocyst-like Organs in a Loxosomatid, Adaptive Developmental Strategies, Host Specificity, and Bipolar Occurrence of Species*

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Abstract. In the southern Weddell Sea and the Bransfield Strait a total of eight species of entoprocts were found: four Loxosomatidae, originally known to be common in the Northern Polar Sea and the Atlantic sector of the subarctic region (*Loxosomella antedonis* Mortensen, 1911, *L. compressa* Nielsen and Ryland, 1961, *L. varians* Nielsen, 1964, and *L. antarctica* Franzén, 1973); three new species of loxosomatids (*L. brochobola* spec. nov., *L. seiryoini* spec. nov., and *L. tonsoria* spec. nov.); and one single colonial entoproct *Barentsia discreta* (Busk, 1886) which is distributed worldwide. *Loxosomella brachystipes*, described by Franzén in 1973 from South Georgia, is shown to be synonymous with *L. varians* Nielsen, 1964. The microscopic investigation of the above species revealed several morphological characters, previously unknown, that add to our knowledge of the Entoprocta in general, and also help in characterizing species. The first of these novel characters, observed in *L. brochobola* spec. nov., are extruding organs similar to cnidarian spirocysts. This is the first description of such organs in entoprocts. *Loxosomella antarctica* is capable of calyx regeneration and thereby becomes the only solitary entoproct known to have such a regeneration capacity. Finally, the formation of special resting buds in *Barentsia discreta* is described. The range of morphological variation of these species, the question of host specificity in the Loxosomatidae, and the bipolar occurrence of some of these species is discussed.

Introduction

Reports on Antarctic Entoprocta are scarce. Until 1973 only five colonial forms had been recorded from the

Southern Ocean, predominantly from the subantarctic region: *Pedicellina australis* Ridley, 1881 was reported from the Magellan Strait, at the Patagonian coast and the Falkland Islands (Islas Malvinas); *Barentsia capitata* Calvet, 1904, and *Barentsia variabilis* Calvet, 1904 were reported from South Georgia and the Falkland Islands; and *Barentsia aggregata*¹ Johnston and Angel, 1940 from Macquarie, Heard, Marion, and the Kerguelen Islands. These latter three species are probably synonymous. Finally, *Barentsia discreta* (Busk, 1886), common circum-antarctically in subantarctic latitudes (Johnston and Angel, 1940; Rogick, 1956; Waters, 1904) as well as on the Antarctic shelf itself, was reported in the Commonwealth Bay (Johnston and Angel, 1940) and from the northernmost tip of the Antarctic Peninsula (Franzén, 1973). In 1973, Franzén augmented these reports with observations of older samples from the 1901–03 Swedish Antarctic expedition. He added *Pedicellina cernua* (Pallas, 1774) and four Loxosomatidae to the list of entoprocts from Antarctic waters: *Loxosomella compressa* Nielsen and Ryland, 1961 var. antarctica; *Loxosomella murmanica* (Nilus, 1909); *Loxosomella antarctica* spec. nov.; and *Loxosomella brachystipes* spec. nov. There have been no more recent studies of the Antarctic entoproctan fauna.

During the Antarctic summer 1989–90, in the course of a survey of the Antarctic benthos supported by the Deutsche Forschungsgemeinschaft, the entoproctan fauna of the Weddell Sea and the Bransfield Strait were investigated aboard the German research vessels PFS POLAR-

¹ A sample of barentsiid colonies from the Californian coast near Santa Cruz, sent me by Kerstin Wasson (University of California, Santa Cruz), proved to consist not only of colonies of *Barentsia ramosa*, being common there, but also of *Barentsia aggregata* J. and A., which had previously been believed to occur only in the subantarctic region.

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STERN and FFS METEOR. Benthic samples were taken in the Weddell Sea at 26 locations along the shelf from its northeastern most edge down to the base of the Antarctic Peninsula. Forty-five hauls were taken with both an Agassiz trawl and an epibenthic sledge (Fig. 1, Table 1). Except at three stations in the 600–1100 m depth range, most samples were taken between 100 and 500 m (see Table I and Fig. 1). The benthic fauna, especially the associations of ciliary-feeders, was generally richer, both in abundance and species diversity, in the eastern part of the Weddell Sea where the steep slope is more exposed to the Weddell Sea current than the fauna of the western Weddell Sea where bottoms are less sloped and less exposed to the current.

In the Bransfield Strait a total of 22 hauls were evaluated, nine from a quadrangular dredge and 13 from a Van Veen Grab, taken at a depth range between 120 and 400 m at 15 locations between Elephant Island to the north and Adelaide Island to the south. (Fig. 2, Table II).

Altogether, eight entoproctan species were found. Four of them occurred in both areas and one species was found only in the Weddell Sea. Three new species were described: two from the Weddell Sea and one from the Bransfield Strait.

As a general trend, the abundance and population density of Entoprocta in the Bransfield Strait was much higher than in the Weddell Sea—presumably because of the higher primary production and consequently higher nutrient supply in this area. Of special zoogeographical interest is that four of the species found to be common in the Antarctic region also occur in the North Atlantic and the Arctic Polar Sea, but seem to be absent from the mid-Atlantic coasts.

Sampling Methods and Treatment of Samples

The trawling times of the sampling gear varied between about 30 and 90 min, according to the bottom structure and ice conditions. To obtain undamaged living samples for laboratory observations and culture experiments, the hauls were immediately subject to rough presorting. Appropriate growth substrates for entoprocts, such as bryozoan and hydroid colonies, bivalve shells, small sponges and stones, as well as potential entoproctan hosts such as errant and sedentary polychaetes with their tubes, sipunculids, echinurans, priapulids, ophiuroids and, occasionally, crinoids, were collected as soon as possible and placed in separate plastic tubs with running fresh seawater of outside

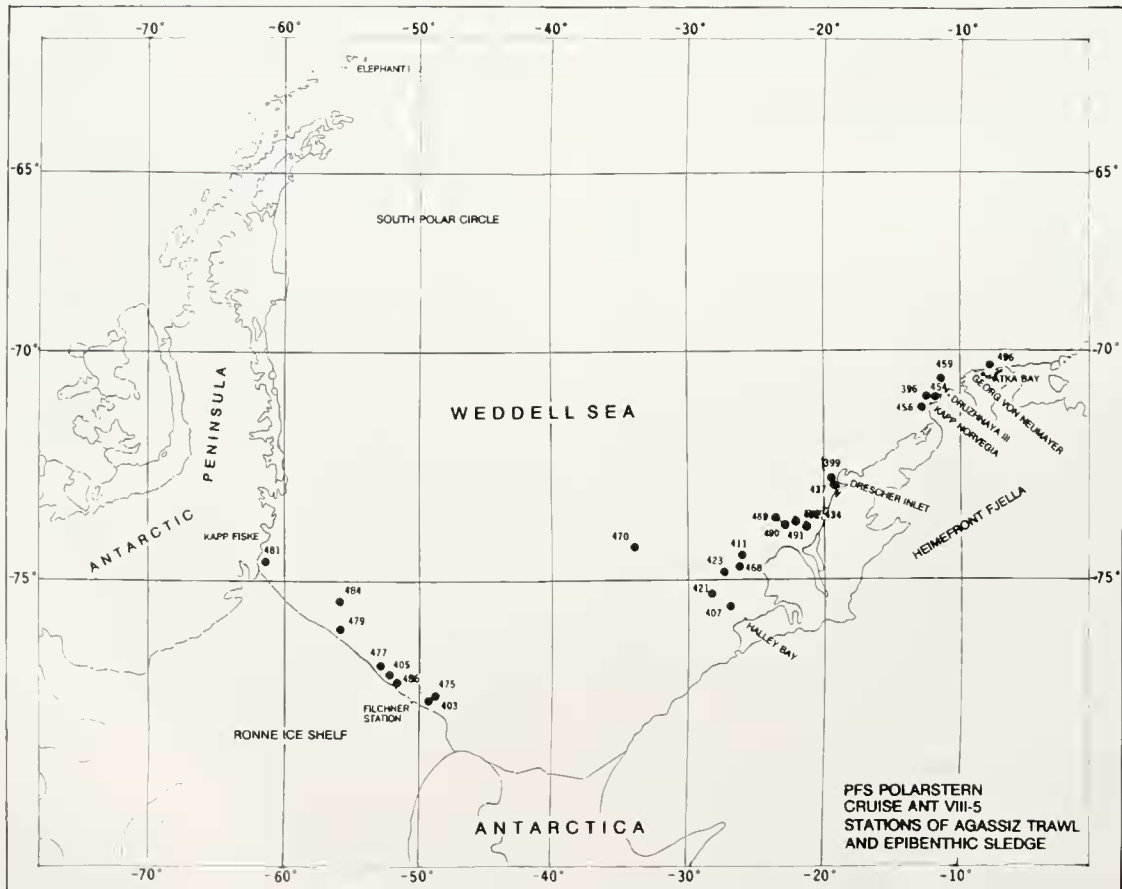


Figure 1. Station map of the POLARSTERN cruise ANT VIII-5 in the Weddell Sea.

Table 1

Station List 1 Polarstern-Cruise ANT VIII-5 in the Weddell Sea

Station	Position	Depth (m)	Date	Gear	Bottom	Predominant fauna
16-396	S 71.08°; W 11.77°	360-320	29/12/89	A	St	Sponges, Bryozoa
-399	S 72.86°; W 19.30°	380-390	30/12/89	A	St, Sf	Sponges, Bryozoa, Ascidia
-403	S 76.94°; W 49.81°	220-250	06/01/90	A	Cb, G	Bryozoa, Holothuria
-405	S 76.52°; W 52.63°	380-390	07/01/90	A	S	Ascidia, Pennatulids, Gorgonia, Sponges; Bryozoa
-407	S 75.46°; W 27.02°	240-250	12/01/90	E, A	Sf	Sponges, Holothuria
-411	S 74.54°; W 25.75°	520-530	14/01/90	E, A	S, St	Crinoids, Holothuria, Nemerteans, Prawns
-421	S 75.21°; W 27.80°	430-400	17/01/90	E, A	S, G	Pennat., Crinoids, Echin., Ophiur., Holothur., Prawns, Fishes
-423	S 74.84°; W 27.56°	460-470	17/01/90	A, E	S, St	Sponges, Pennat., Ophiur., Prawns
-434	S 73.69°; W 21.75°	260-270	20/01/90	E, A	Cb, St	Bryoz., Holoth., Prawns
-437	S 72.84°; S 19.40°	390-420	21/01/90	E	Cb, St	Bryoz., Ophiur., Amphip.
-454	S 71.08°; W 11.69°	210-280	26/01/90	E, A	Sf	Sponges, Gorgon., Fishes
-456	S 71.25°; W 21.01°	200-250	26/01/90	A, E	Sf	Sponges, Ascid., Amphip., Fishes
-459	S 70.69°; W 11.19°	350-390	28/01/90	E, A	G, St, Cb	Sponges, Pennat., Crinoids, Amphipods
-468	S 74.74°; W 26.36°	480-460	09/02/90	E, A	S, G	Pennat., Amphip., Prawns, Fishes
-470	S 74.28°; W 34.09°	1050-960	10/02/90	E, A	Cb	Stylasterids, Ophiur., Ascid., Sponges, Polychaetes
-475	S 76.85°; W 49.45°	280	13/02/90	E, A	S	Sponges, Echin., Ascid., Crin.
-477	S 76.45°; W 53.15°	430-450	14/02/90	A, E	S	Pennat., Echin., Prawns
-479	S 75.68°; W 56.72°	340-360	14/02/90	E, A	S, Sf	Crin., Ophiur., Prawns, Pantop.
-481	S 74.71°; W 61.14°	640-620	15/02/90	A, E	St	Ophiur., Amphip., Prawns
-484	S 75.28°; W 55.98°	450-440	16/02/90	E, A	S	Pennatul., Ascid., Ophiur., Polychaetes, Brachiopods
-486	S 76.50°; W 52.15°	340-330	17/02/90	E	Cb	Spong., Bryoz., Pennat., Ascid.
-489	S 73.68°; W 23.13°	980-990	21/02/90	A	St	Ophiuroids, Prawns
-490	S 73.70°; W 22.66°	630-610	21/02/90	E	Sf	Crin., Holothur., Echin., Prawns
-491	S 73.69°; W 22.42°	390-370	21/02/90	E	S, G	Crinoids, Pantopods, Amphip.
-492	S 73.69°; W 21.74°	250	21/02/90	A	Cb	Crin., Bryoz., Spong., Ophiur.
-496	S 70.63°; W 08.09°	80	27/02/90	A, E	Cb	Bryozoa, Holothuria

Benthos stations: Gear, sediments, and predominant fauna

Gear: A, Agassiz trawl; E, epibenthic sledge; Bottoms: Cb, calcareous bryozoan shells; G, sand and coarse gravel; S, sandy silt and mud; Sf, felt of sponge needles; St, larger stones and rocks.

temperature (-1 to +0.5°C). The presorted substrates were subsequently checked for entoprocts under the dissection microscope. About half of the zooids of each species found were kept alive, whereas the rest of them were preserved, some after narcotization, some without such a pretreatment.

Narcotization and fixation

A 4% formaldehyde solution in seawater proved to be the best fixation medium, yielding usable results even for electron microscopical purposes. For fast narcotization, especially when specimens were treated while still on their host, the gradual addition of an isosmotic solution of MgSO₄ gave acceptable results. But the local anesthetic amylocaine-hydrochloride [Stovaine^R Rhone Poulenc: 1-(dimethylamino)-2-methyl-2-butanol-benzoate hydrochloride] was more effective, particularly for small samples or single specimens in a small amount of water. By far the best results were obtained with a two-step narcotization: 8-10 crystals of amylocaine-hydrochloride were

gradually added to a small sample of specimens in about 2 ml of seawater until the animals were completely expanded and showed no reaction to mechanical stimulation (about 10 min). Subsequently, some crystals of MgSO₄ were added. After 5 min the sample could be fixed by the addition of 0.2 ml of 4% formaldehyde.

Treatment of living samples

Living samples for later culture experiments and observations aboard were kept in 5-10 l aquaria under running seawater at 0-0.5°C on their original substrates or hosts. They were fed by the moderate addition of fresh nanoplankton samples, chiefly diatoms. Only the colonial *Barentsia discreta* could be cultured successfully and brought home to the laboratory still alive. None of the solitary loxosomatids could be kept alive and actively budding for more than three to four weeks, even when left on their original hosts.

Measurements and sketches

Measurements of a representative number of living specimens (30-50 if possible) from every locality were

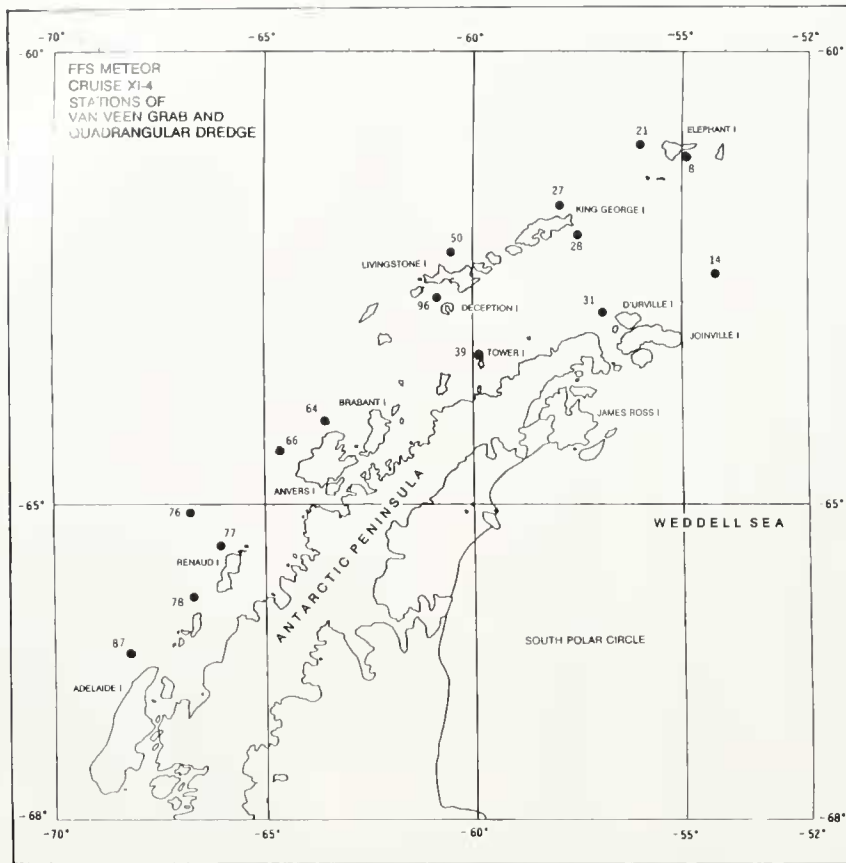


Figure 2. Station map of the Meteor cruise XI-4 in the Bransfield Strait.

taken aboard and, later on, compared with those of random samples of preserved specimens. These groups of measurements were not significantly different. Freehand sketches were made of living specimens. When ship conditions allowed, micrographs of living specimens were taken through the dissection microscope. Higher magnification micrographs were made from preserved material in the home laboratory.

Some Remarks on Species Determination and the Description of New Species in Entoprocta

Entoprocta in general, and most Loxosomatidae in particular, have a scarcity of reliable species characters. The majority of morphological parameters, such as size, number of tentacles, body proportions, shape of stomach, and even conspicuous structures like cuticular pores, and spines, and body appendices, exhibit great intraspecific variability, and there is often overlap between species. Because of this deficiency of reliable morphological features, attempts have often been made to use the host or the locality of an entoproct as an aid for identifying its species. But neither the number of true species and their variation, nor their geographical distribution and possible

spectrum of hosts, are sufficiently well-known to be useful in species identification.

A rigorous biological species characterization by demonstration of their genetic isolation has not been possible for the great majority of entoproct species. Therefore, any species determination, especially any description of new species, founded on the evaluation of a few morphological characteristics, should be based on an intimate knowledge of all comparable species and, if possible, a comparison of the specimens in question with the type material of all similar species or, at least, with definitively identified samples of the latter. The description of a new species is not of value in itself; the demonstration of the real distribution range of a species is much more important.

Any description of specimens new to an area should be illustrated with precise drawings in frontal and lateral view, and, if possible, in the contracted as well as the expanded state. Additional micrographs are often very helpful. Proof samples or types should be preserved both in contracted and expanded state. Because of insufficient description and unsatisfactory preservation of type material, not one Loxosomatidae described by Harmer (1915) from the Siboga samples can be reidentified.

Table II

Station List 2: Meteor-Cruise XI-4 to the Bransfield Strait

Station	Position	Depth (m)	Date	Gear	Bottom
08-90	S 61.25° W 55.05°	125	29/01/90	VG	S
14-90	S 62.53°; W 54.15°	400	29/12/90	VG, D	St
21-90	S 61.00°; W 56.00°	337-426	30/12/90	VG	S
27-90	S 61.75°; W 57.89°	340	01/01/90	VG	S
28-90	S 62.09°; W 57.64°	286-383	01/01/90	VG	S
31-90	S 62.99°; W 56.99°	80	02/01/90	VG, D	St, S
39-90	S 63.42°; W 59.86°	155	03/01/90	VG, D	St
50-90	S 62.25°; W 60.57°	167-147	05/01/90	VG, D	S
64-90a	S 64.15°; W 63.55°	135-150	08/01/90	VG, D	St
66-90	S 64.47°; W 64.77°	356	08/01/90	VG, D	St, S
76-90	S 65.06°; W 66.98°	220	10/01/90	D	St
77-90	S 65.39°; W 66.18°	330-370	10/01/90	VG	St
78-90	S 65.91°; W 66.85°	75	11/01/90	D	St
87-90	S 66.57°; W 68.57°	450	12/01/90	VG, D	S, St
96-90	S 62.77°; W 60.90°	150	16/01/90	VG, D	S, St

Benthos stations: gear and sediments

Gear: VG, Van Veen grab; D, rectangular dredge; Bottom: Cb, calcareous bryozoan shells; G, sand and coarse gravel; S, silt and mud; Sf, felt of sponge needles; St, larger stones and rocks.

Because of our limited knowledge of the intraspecific variability and geographic distribution of most entoproctan species, every describer of a new entoproctan species should be wary that his new species may turn out to be synonymous with a species long known, even if all precautions have been taken. The following descriptions of new species must be seen in this light.

Description and Discussion of Species

Loxosomella brochobola spec. nov.

Holotype. Collected by the author on 20 January 1990 at the type locality, stat. 16-434 ANT VIII-5 (73.69°S; 21.75°W) at a depth of 260–270 m from sandy and rocky bottoms with abundant calcareous Bryozoa; the entoproctan species was growing exclusively on the inner, abfrontal surface of tube-shaped *Porella malouinensis* colonies (Bryozoa).

Syntypes. Deposited in the British Museum of Natural History, London (No. 1992.12.14.1) and the Zoologisk Museum, Kobenhavn.

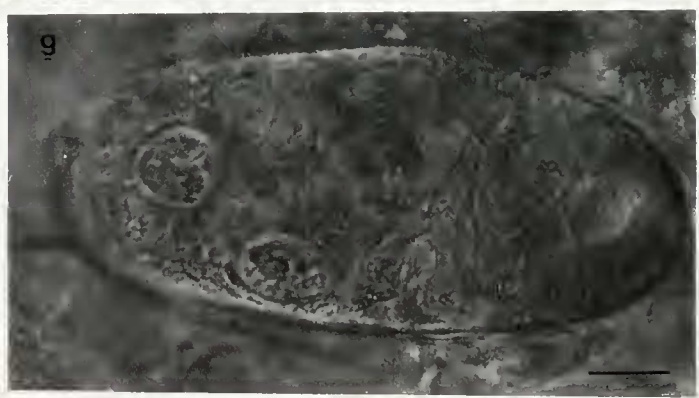
Name. From Greek: βροχοζ-snare and βαλλειν-discharge, referring to the sticky threads that can be ejected by nematocyst-like extrusive organs—a unique character of this species.

Description. This is a tall *Loxosomella* species, about 1300 μm in length, the individuals resemble at first glance a *Pedicellina* zooid (Figs. 3a–c; 4). The bulgy goblet-shaped calyx is sharply delineated from the long, slender, and highly motile stalk. The large tentacular crown with 14–20 slim tentacles is oriented straight up. In the expanded state, the calyx is slightly laterally depressed, but is nearly globular when contracted. The rectum bulges out between the aboral pair of tentacles, and the anus opens immediately anterior to the aboral ends of the

horseshoe-shaped peritrial ciliary rim (Fig. 4f, i). The peduncle is slender, cylindrical and one and a half to twice as long as the calyx. About halfway down there is usually a slight “waist.” The basal attachment area is narrower than the average diameter of the peduncle and animals are not fixed very strongly to their substratum, but can be removed easily without damage. Remnants of the foot gland normally persist as a plug of globular cells in the base of the stalk. As often observed in loxosomatids, the perikarya of the peduncular epithelial cells are arranged in longitudinal rows between the muscle strands.

The stomach is voluminous and globular with wide lateral pouches bulging out at either side (Fig. 4k). The longitudinal musculature of the oral side consists of a dense layer of fibers running downwards from the oral and orolateral calyx wall to nearly the base of the peduncle, while at the aboral side and laterally in the upper portion of the stalk, only 2–3 single strands at either side are developed. Basalwards these aboral muscle fibers increase in number, thus forming—together with the oral fibers—a closed muscular tube in the lower portion of the peduncle.

Living specimens in normal expanded posture have the peduncle slightly curved, the aboral side of the calyx inclined downwards, the oral side up (Fig. 4f). Seen from above in this position, four large whitish blue, opaque blister-like structures are conspicuously visible at either side between the bases of each of the second and third, as well as the third and fourth, oral tentacle. Upon irritation, or sometimes spontaneously, 300–400 μm long delicate, helically twisted threads can be ejected from these enigmatic organs (Figs. 3d–h; 4b–d, n–g), which resemble



cnidarian spiro- or nematocysts. The sticky threads are as long, or somewhat longer than the tentacles, and remain anchored with their proximal ends in the epithelial cells from which they originate, floating with their distal ends, outside the tentacular crown. At higher magnification these extrusive organs each consist of an enlarged barrel-shaped and plurinuclear epithelial capsule, about 80 μm long and 45 μm in diameter. In the unexploded state, it is filled with an invaginated highly coiled tubule, roughly square in cross section. The nuclei, generally four, are situated basally in a narrow area of marginal plasma. When ejected, the evaginated tubule, about 3 μm in diameter, has an X-shaped cross section and is covered by a thin mucous coat. *Loxosomella brochobola* is the only entoproct known to have such extrusive organs.

The function of these organs is obscure, but defense seems unlikely. Possibly these extrusive threads are connected with a specialized method of feeding; their arrangement around the mouth supports such a presumption. The extrusive threads could act as a kind of "fly paper" in a marine biotope poor in suspended matter. They would collect small particles attached to the substratum and inaccessible to the ciliary feeding apparatus, and from time to time would be swallowed together with any adhering material. But this kind of activity has, so far, not been observed.

From their genesis, the extruding organs are surely true kamptozoan organs, not "kleptocnides" somehow acquired from hydroids growing in their immediate vicinity, such as *Halecium*. Moreover, in both their overall structure and extrusion mechanism, they are distinct from similar cnidarian organs. Unlike the tubules of cnidarian nematocysts, they do not evaginate by turning inside out, like a glove finger, but rather they are ejected simply by the unfolding of the curled introverted thread through a rupture of the extruding capsule at its proximal tip. (An ultrastructural investigation of these peculiar organs is in progress and will be published separately.)

Buds, normally two to three on either side, develop orolaterally, level with the basal half of the stomach. They are fixed to the parent, not by the aboral tip of the foot, but by a junctional zone situated basally at the aboral side of the calyx, as is known from *Loxosomella kefersteini* (Figs. 3a, d; 4a-e, l). The long, sickle-shaped glandular foot of the bud points upwards. The main body of the foot gland is situated just below the stomach. From there,

a narrow glandular groove bordered by large secreting cells runs all along the foot to its aboral tip. After the bud has detached from the parent, the foot does not degenerate totally, but develops into the basal portion of the adult peduncle. The aboral tip of the foot becomes the attachment site for settling on the substrate. The upper portion of the adult stalk above the "slight waist" consequently develops by stretching the zone between the calyx base and the proximal part of the foot.

Gonads in different stages of development were observed in nearly all specimens examined: Immature and mature testes were developed only in undetached buds and newly settled specimens, while mature ovaries were found exclusively in larger animals, usually with 1-2 eggs on either side. The testes are positioned laterally to the stomach; the ovaries lie more distally, in the space between stomach, esophagus and the atrial bottom. In a few specimens unhatched larvae lacking eyespots were observed (Fig. 4m).

Measurements: Total length: 1200 μm (994-1350 μm); length of calyx: 380 μm (260-493 μm); length of stalk: 800 μm (423-978 μm); width of calyx: 335 μm (239-408 μm); thickness of calyx: 400 μm (245-554 μm); diameter of stalk: 90 μm (65-114 μm); number of tentacles: 18 (12-20), in buds: 12.

Habitat and distribution. Though its bryozoan host is abundant all over the Weddell Sea, *Loxosomella brochobola* has been found at only two locations in the eastern Weddell Sea (stations ANT-VIII-5 16-396; 16-434; 16-491; and 16-492). *L. brochobola* grows exclusively on the inner, abfrontal surface of the tube-shaped colonies of *Porella malouinensis* (Bryozoa) which is sometimes associated with young colonies of an undetermined species of *Halecium* (Hydroida). At the type locality *L. brochobola* was growing in small groups of 20-30 specimens/cm², specially on younger host colonies settled only sparsely by other epizoans.

Discussion of the species. The loxosomatid described above is the only entoproct known to possess nematocyst-like organs. These may be homologous to and derived from pearl-like glandular cells or cell complexes, which have been found to be more or less regularly scattered around the margin of the tentacular crown in a number of loxosomatids. These organs alone are a striking species character. To date only four other loxosomatids are known which show the budding pattern described above: *Loxosomella kefersteini* Claparède, 1867, *L. pseudocompressa* Konno, 1977, *L. annulata* Harmer, 1915, and *L. mepse* du Bois-Raymond-Marcus, 1957. In its general appear-

Figure 3. *Loxosomella brochobola* spec. nov. a-c: living specimens in abfrontal (a) and lateral view (b, c); d: contracted specimen with large bud and ejected sticky threads; e: ejected sticky thread; f: extrusion organ in Nomarski contrast, the coiled ejectable tubule is visible (bar 10 μm); g: the same organ, two of four nuclei are visible at the left side (bar: 10 μm); h: part of an ejected tubule [bar in all micrographs 100 μm unless otherwise indicated].

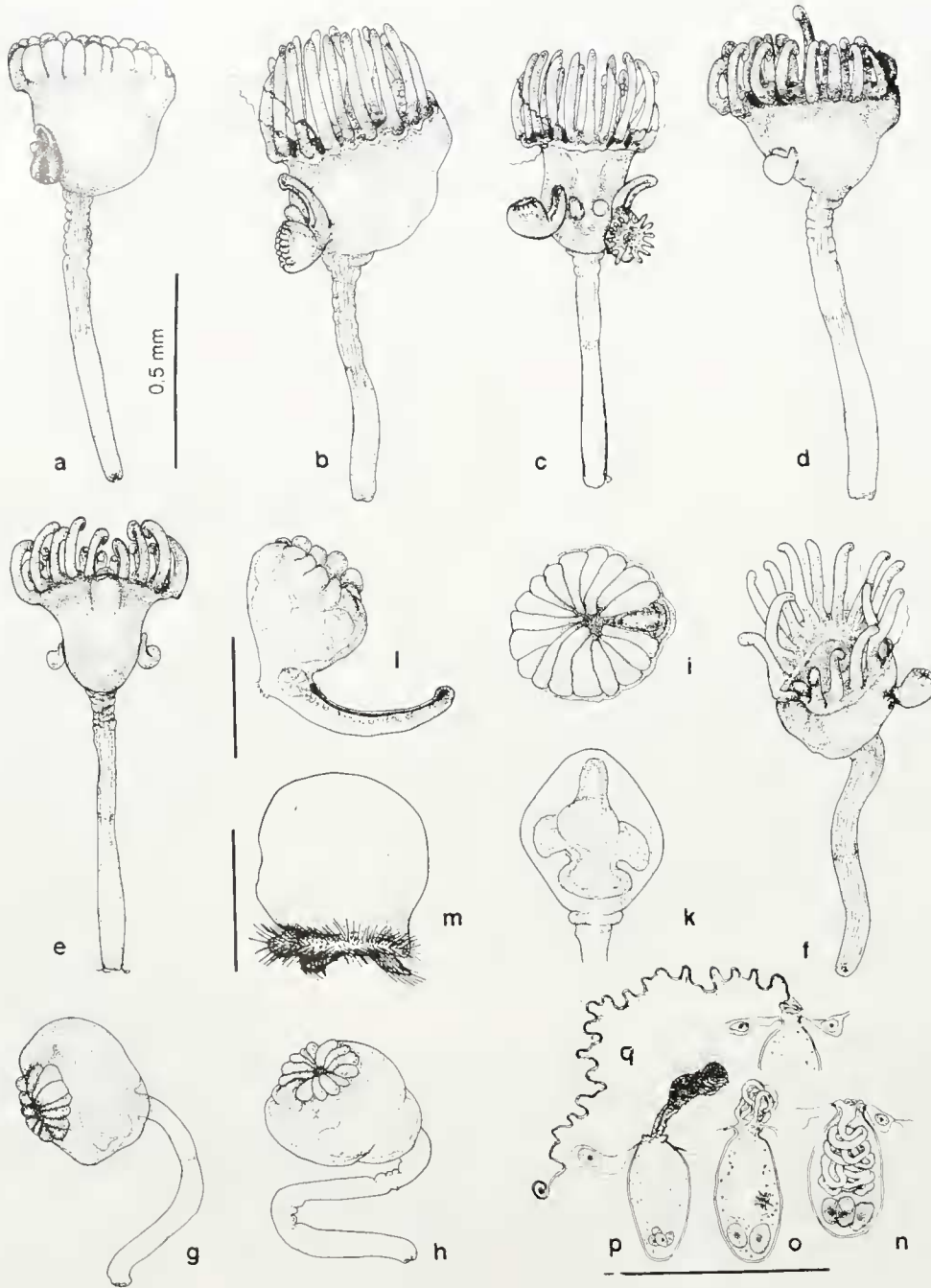


Figure 4. *Loxosomella brochobola* spec. nov. a: contracted zooid from fixed sample; b–e: two expanded zooids (b/c; d/e), in lateral-frontal, and lateral-abfrontal view, respectively, with buds and, partly, ejected extrusion organ; f: living expanded zooid in normal posture; g, h: bending movements of a zooid after irritation; i: contracted tentacular crown seen from above, the rectum bulging out between the aboral tentacles; k: calyx seen from the aboral side; lateral pouches of the stomach are visible; l: newly detached bud, the navel being visible at the abfrontal side of the calyx base; m: young larva before hatching; n–q: extrusive organs in different stages of ejecting the sticky thread (from preserved specimens).

ance, only the latter shows some similarities to the Weddell Sea specimens; but the smaller size and average number of tentacles of *L. mepse*, the shape of its stomach not being trilobed, the shorter foot of its buds not being sickle-

shaped, and most of all, the lack of the conspicuous extrusive organs clearly distinguishes this species from the Weddell Sea specimens. In conclusion, *Loxosomella brochobola* is a reliable new species.

Loxosomella seiryoini spec. nov.

Holotype. Collected by the author on 17 January 1990 at the type locality, station 16-421 ANT-VIII-5 (75.21°S; 27.56°W) at a depth of 430–470 m from a silty and muddy bottom; specimens were growing in dense populations on the rear end of the body and the anterior part of the proboscis of *Golfingia margaritacea* (Sipunculida). Four of eight specimens of this particular sipunculan species, depending on their size, were host to 20 to several hundred loxosomatids.

Syntypes. Deposited in the British Museum of Natural History (no. 1992.12.14.2) and in the Zoologisk Museum Kobenhavn.

Name. The species name is given in honor and remembrance of a Japanese friend and colleague who passed away.

Description. *Loxosomella seiryoini* is a small species, with club-shaped individuals about 700 μm long. The calyx, almost circular in cross section, gradually transforms into a peduncle of half to one times the calyx length, tapering slightly towards its base and affixed to the substratum by an enlarged attachment disc (Figs. 5a–e; 6). The tentacular crown, with eight short, stoutish tentacles, is inclined oralwards in an angle of about 45°, both in contracted and expanded state, and is surrounded by a broad peritentacular membrane resembling a Stuart-collar in expanded animals. In living specimens, this collar is much more conspicuous than in preserved ones, where it is manifested merely as a swelling of the lophophoral rim (Fig. 6a, c).

The calyx tapers gradually into the stalk when expanded, but in strongly contracted specimens a deep fold demarcates the transition between calyx and peduncle, and the latter becomes bulgy and barrel-shaped. The footplate is fixed very firmly to the substratum by a thin brownish layer of the foot gland secretion, and in some cases a small remnant of this gland persists as a small globular pit in the middle of the adhesive disc (Fig. 5e).

Specimens settling on the introvert of the host usually are enclosed by a felty and stiff cuirass of adhering detritus particles which are permanently agglutinated with the cuticle, leaving only the lophophoral area and the oral side uncovered (Fig. 6i–k). Such individuals have a considerably reduced capacity for expansion, and they have a more sturdy, globular shape with a short bulging peduncle.

The stomach is globular in outline and lacks lateral pouches. The longitudinal musculature consists of about 12 coarse muscle strands running down from the oral calyx wall to the foot plate, as well as some more delicate lateral and aboral fibers. In the basal portion of the peduncle, particularly in contracted specimens, 10 to 12 additional delicate spirally arranged fibers can be observed (with polarized light!); these fibers crisscross in opposite directions, forming a helical lattice. The buds—usually one at either side of the calyx—develop orolaterally, in line with the base of the stomach. When mature enough to become detached, they have only a short, boat-shaped foot-gland (Figs. 5c; 6d).

In most specimens, gonads in different maturation stages are present: immature testes in undetached or newly detached buds, ovaries in older specimens and, sometimes, embryos and larvae in the brood pouches (Fig. 6f, g). Occasionally, ovaries with eggs as well as degenerating testes were observed in the same specimen, indicating that this species, like other loxosomatids, is protandric.

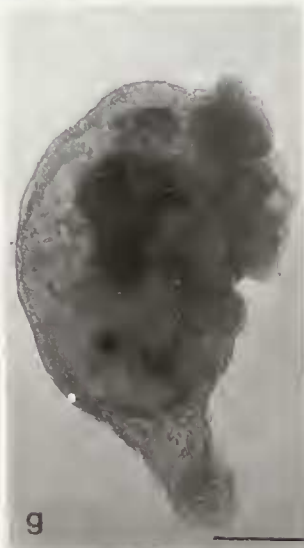
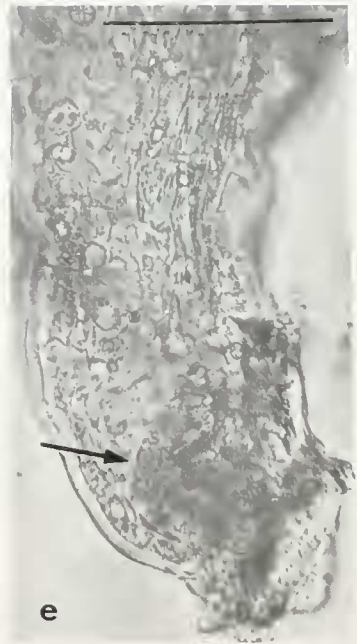
Measurements. Total length: 700 μm (560–780 μm); length of calyx: 400 μm (318–415 μm); length of peduncle: 270 μm (163–318 μm); width of calyx: 280 μm (160–350 μm); thickness of calyx: 290 μm (254–349 μm); diameter of peduncle: about 124 μm above, tapering to 100 μm at its base; number of tentacles: 8.

In one single, older, not very well preserved sample (stat. 224, Ant VII/4, 71°15'S; 13°07'W) on a specimen of *Golfingia margaritacea*, a number of loxosomatids were found that are similar to *L. seiryoini* in most characters (calyx shape, swollen lophophoral rim, the helical muscular lattice, and remnants of the foot-gland in the peduncular base) except that they have a long, slender peduncle (about 1000–1400 μm) and thus achieve a total length of 1400–2000 μm . Whether *L. seiryoini* really attains such a size, or whether these specimens were artificially stretched by rude handling during sorting and preserving, is unclear.

Habitat and distribution. *Loxosomella seiryoini* has been found exclusively on *Golfingia margaritacea* in the Weddell Sea, never on other sipunculans of the same size occurring at the same sites. West of the Antarctic Peninsula this loxosomatid seems to be absent, although the host is as common in this region as in the Weddell Sea. This *Loxosomella* preferably settles at the rear of its host and around the foremost part of the introvert where, in most cases, it is difficult to detect. Especially at the latter site, it can form crowded aggregations.

Discussion of the species. This loxosomatid is one of numerous medium-sized species, that lack striking species characters. Quite a list of such species with 8 tentacles and a more or less club-shaped form exists in the literature. Most of these species cannot be reidentified due to the poor quality of the original description—based in some cases on only a single specimen—and due to the insufficient preservation, or the complete lack of any type material. This applies to: *Loxosomella breve* and *L. loricatedum* (Harmer, 1915) from the Siboga samples; *Loxosomella mimuta* Osburn, 1910, described from the Woods Hole region as growing on sipunculids; *Loxosoma* (*Loxosomella*?) *cingulata*, *L. infundibuliformis*, and *L. rotunda*, described by Kluge (1946) from the Arctic Polar Sea; and *Loxosoma* (*Loxosomella*?) *singulare* Barrois, 1877 and *L. singulare* Hincks, 1880. However, Harmer mentions small lateral sensory papillae present in the Siboga specimens; so they seem to be different from our species.

Among the more recently described species, *Loxosomella fauveli* Bobin and Prenant, 1953, *L. globosa* Bobin and Prenant, 1953, and *L. varians* Nielsen, 1964, look similar to the Weddell Sea form. But even if one does not attach too great significance to their smaller size and divergent hosts, a number of other characters differ considerably from *L. seiryoini*: they all lack the conspicuous



collar-like peritentacular membrane; all normally have more than 8 tentacles, except *L. varians*; and the buds of only the latter have a small, partly reduced foot-gland. *L. seiryoini* and *L. varians* on the other hand differ in the shape of the extended adult foot plate, which is bordered by conspicuously large cells in *L. varians*, but which are lacking in *L. seiryoini*. Furthermore, the helically arranged muscle strands in the basal portion of the peduncle of the latter seem to be absent in *L. varians*. So at present, *Loxosomella seiryoini* may be regarded as a new species.

Loxosomella tonsoria spec. nov.

Holotype. Specimens were collected by Dr. U. Wirth on 8 January 1990 at the type locality, station 66/90 Meteor XI-4 (64°30'S, 64°45'W) at a depth of 320 m from a stony and muddy bottom, growing in small numbers (10 specimens) dorsally on the anterior segments and gills of an ampharetid polychaete (cf. *Glyphanostomum* spec.; Fig. 7a, b).

Name. From Latin: tonsorius-shaver, because of the gibbous appearance of the calyx, which in lateral profile resembles an old Norelco® electric shaver (e.g., Fig. 5f).

Description. A medium-sized species, 600–800 μm in length, with a characteristic gibbous calyx, a short and thin peduncle of about 0.5–0.7 times the calyx length. The comparatively large tentacular crown with 8 short and stout tentacles faces towards the oral side (Figs. 5f–i; 7e–f).

The calyx is slightly laterally depressed (width/thickness ratio 0.8). Below the stomach, the calyx constricts abruptly into the thin peduncle, which tapers somewhat towards its base and terminates in a small attachment area. The latter consists of a small epithelial invagination representing a remnant of the genuine foot-gland (Figs. 5k; 7h, i). The animals are not fixed very firmly to their substratum and can be easily removed without damage; they fall off easily after fixation. The stomach is almost globular, and as a result of the humpbacked calyx, the rectum is an unusually long tube.

The longitudinal musculature consists of only a few muscle strands: frontally and at either side 2 to 3 fibers each run from the calyx wall down to the base of the peduncle. Buds develop orolaterally in line with the upper half of the stomach. Only two of the specimens had developed very young buds, however, since these did not show any trace of a foot-gland, nothing is known of its structure.

Mature gonads (Fig. 7g, f) were present in all specimens; the majority contained ovaries with 3–4 eggs in different

maturation stages. In one single case, testes filled with sperms were observed and in another specimen, the remnants of degenerating testes were visible below the ovaries. This indicates a protandric hermaphroditism also in this species.

Measurements. Total length: 600 μm (366–795 μm); length of calyx: 370 μm (223–461 μm); length of peduncle: 197 μm (95–350); width of calyx: 200 μm (111–240 μm); thickness of calyx: 243 μm (223–254 μm); diameter of peduncle: 95 μm (above) to 64 μm (below); number of tentacles: 8.

Habitat and distribution. Only 10 specimens of this loxosomatid were found on the gills and the dorsal side of the first segments of an ampharetid polychaete from silty and rocky bottom, west of Anvers Island at a depth of 320 m.

Discussion of the species. Since a small foot-gland is present even in adult specimens (Figs. 5k; 7h, i)—a remnant of a presumably larger gland in the buds—the above specimens belong to the genus *Loxosomella*. The rudimentary attachment gland seems to remain active throughout life. Any conspicuous circular muscle fibers in the peduncle base, which would indicate a sucker-like function of the basal glandular pit, as is characteristic for the genus *Loxosoma*, are lacking. The body shape is quite distinctive: no other loxosomatid so far described has such a gibbous calyx with the expanded tentacular crown facing exactly towards the front. The species characterization is based on only a few individuals; additional examination of the foot-gland structure in older buds, as well as an investigation of the variation range of this species from more numerous samples is highly desirable. The data available at present suggest that the specimens described above constitute a new species.

While nothing is known so far about the distribution of the above new species beyond their type localities, the species described below seem to be distributed not only in the whole Atlantic sector of the Antarctic and subantarctic sea, but also in the arctic and subarctic region of the northern hemisphere.

Loxosomella antarctica Franzén 1973

Material. Collected by the author in the Weddell Sea at stations ANT VIII-5/16-396, 16-411, 16-421, and 16-434, growing on the brittle star *Ophiurolepis gelida* as well as on the aphroditid polychaete *Laetmonice producta* at stations 16-411 and 16-489. In the Bransfield Strait the species has been found by Dr. U. Wirth at the stations Met. XI-4/31-90, 39-90, and 64-90 growing on the same hosts with an apparent preference for *Ophiurolepis gelida*.

The original description of this species given by Franzén (1973) was based on preserved specimens from samples

Figure 5. *Loxosomella seiryoini* spec. nov. a–e: contracted preserved specimens in frontal view (a), and lateral view (b); c: specimen with large bud; d: contracted specimen with a small bud; e: stalk of the latter with basally visible remnants of the foot-gland (arrow); f–k: *Loxosomella tonsoria* spec. nov., preserved specimens in lateral and frontal view; i: with a small bud; k: stalk of i with basal remnant of the foot-gland (arrow) [bar 100 μm].

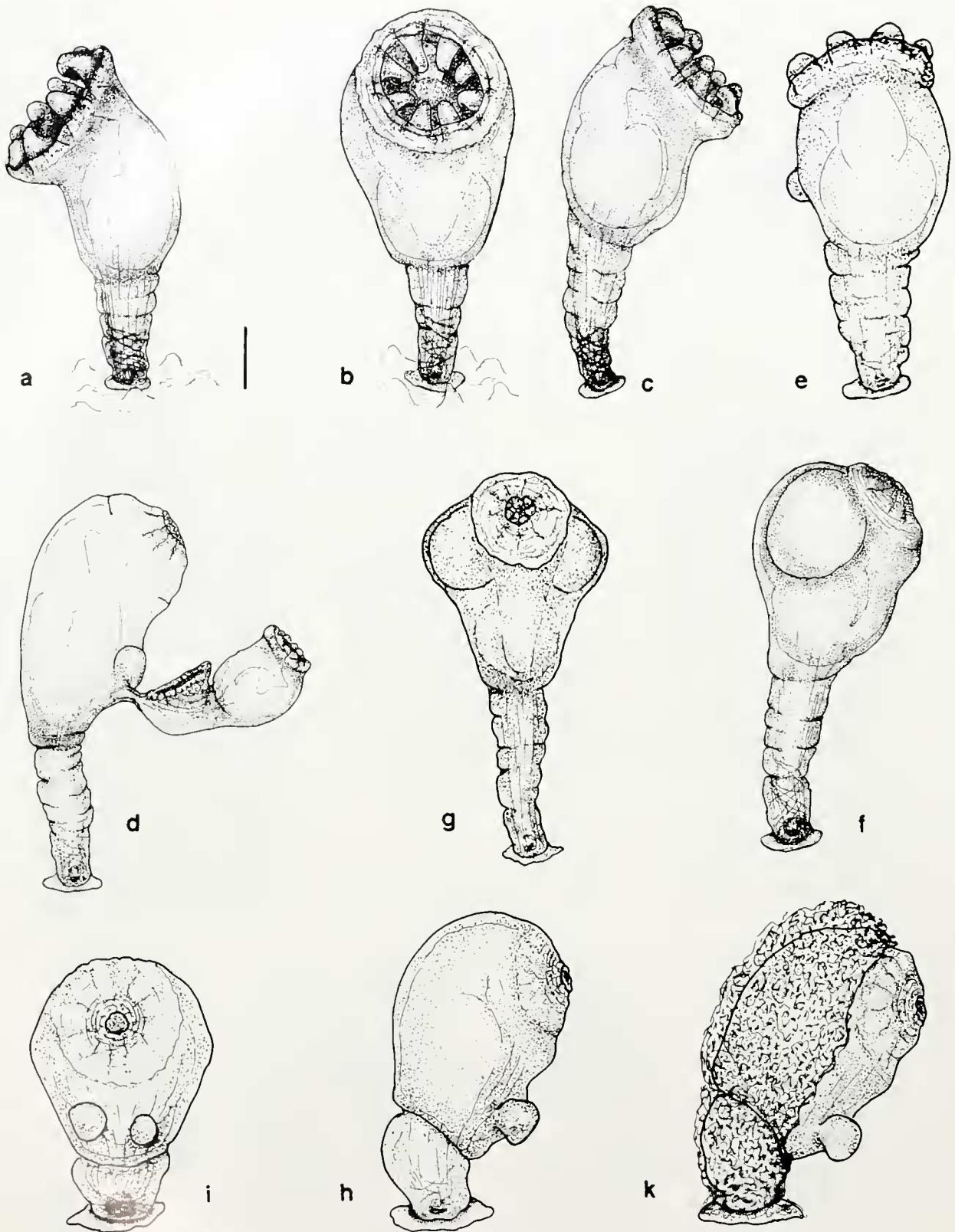


Figure 6. *Loxosomella sciryonni* spec. nov. a–g: different zooids from the rear end of *Golfingia margaritacea*. a: living specimen with the conspicuous peritentacular collar; b and c: preserved specimens; d: contracted specimen with large bud; e: specimen in semiexpanded state, in abfrontal view; f and g: specimens with larvae in their brood pouches in lateral and frontal view, respectively; h–k: different specimens from the introvert of the host, k with a robust “lorica” out of detritus particles covering the abfrontal part of calyx and stalk. In the foot plates of all specimens remnants of the foot-gland are visible.

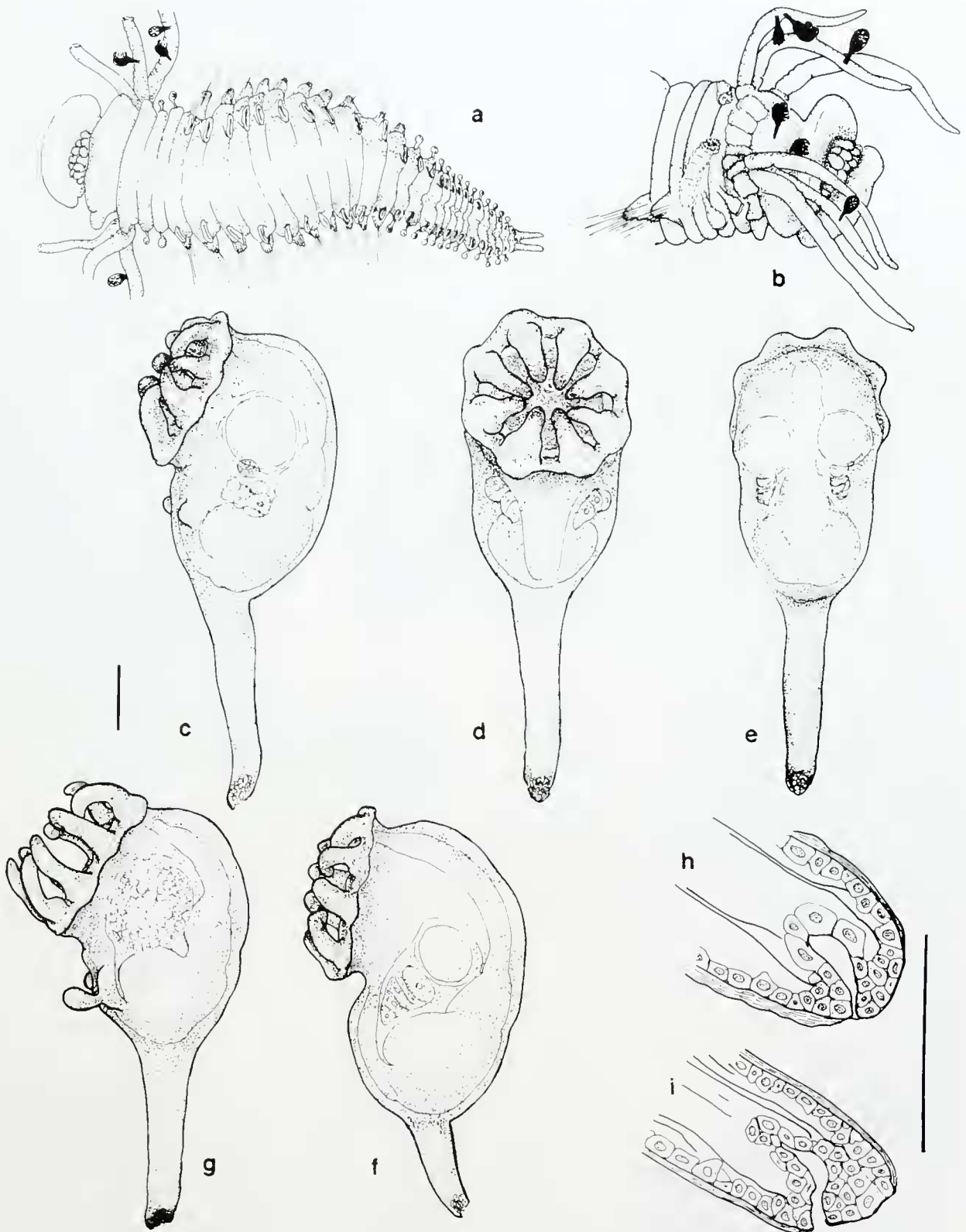


Figure 7. *Loxosomella tonsoria* spec. nov. a: host polychaete *Glyphanostomum* spec.; b: head region of the latter with loxosomatids settling on the cirri and the prostomium; c-e: preserved expanded specimen with mature ovaries, in lateral, frontal, and abfrontal view, respectively; f and g: preserved specimens in lateral view with mature ovary (f) and mature testes (g); h-i: basal tip of the stalk with remnants of the foot-gland.

of the 1902 Swedish Antarctic Expedition; these samples were dredged west of the northernmost tip of the Antarctic Peninsula. Franzén's description will be supplemented by my recent observations on living specimens.

Description. *Loxosomella antarctica* is a tall species, up to 2 mm in length, with a high goblet-shaped calyx, almost lyriform when seen from the oral side, and nearly circular in cross section. Only in a strongly contracted state is it at times somewhat flattened (Figs. 8a–f; 9a–g). In the expanded state, the large tentacular crown, generally with 12 slender tentacles (only 10 in newly detached buds), is inclined to the oral side at an angle of about 45°; when contracted it faces more or less orally. The peduncle of large budding specimens varies in length from $\frac{2}{3}$ to 3 times the calyx length. Basally, below a conspicuous constriction, it terminates in an enlarged foot-plate.

The stomach is variable in shape, voluminous and globular to inversely triangular, but in contracted specimens, transversely oval. The cuticle is comparatively robust; in younger specimens it is smooth, but in older individuals, especially in the basal portion of their peduncle, broadly wrinkled. The body musculature is well developed. Longitudinal fibers run upwards from the peduncular base, fanning out into the calyx where, at either side of the esophagus and intestine, they insert into the frontal and aboral body walls. The muscular layer, compact at the oral side, thins out towards the aboral side into loose bundles of single fibers.

Depending on the nutritional conditions, 1–3 buds appear at either side (Fig. 9f), developing anterolaterally in line with the middle of the stomach. The glandular foot of the bud has a long posterior extension and only a knob-like frontal protuberance (Figs. 8e; 9h). This is one of the striking differences between this species and the similar-looking *Loxosomella antedonis* (Fig. 14e), which is difficult to distinguish from younger specimens of *L. antarctica*. But in the buds of the former, the foot is inversely T-shaped, extending to a conspicuous anterior as well as a posterior, process. Immature and mature gonads are present in most specimens—testes exclusively in buds and newly detached specimens, and ovaries only in older zooids.

So far the Weddell Sea and Bransfield Strait samples agree quite well with Franzén's description and illustrations. But the variability in the ecological conditions of the Weddell Sea, and, consequently, in the size and body shape of the Weddell Sea specimens, is much higher than in the type samples. While the average size of Weddell Sea specimens is about 1000 μm (600–1750 μm), the Bransfield Strait samples average 1500 μm (640–2100 μm), and both are smaller than Franzén's specimens. The calyx of the latter is, in most cases, distinctly marked off from the peduncle, but in some Weddell Sea populations it transforms gradually into the stalk. In these samples, the stalk usually tapers towards its base to about half of

its original diameter (Figs. 9i–l; 10c, d), while in Franzén's samples, the stalk was cylindrical throughout its length. According to Franzén, *Loxosomella antarctica* lacks any lateral sensory papillae. But in two Weddell Sea populations (stat. 16-422 and 16-439), in a number of specimens growing on *Ophiurolepis gelida*, very small sensory papillae were present on either side of the calyx, in line with the second pair of oral tentacles (Figs. 9i–l; 10c, d). Usually these delicate "sensory spots" are only visible under higher microscopical magnification as pointed cuticular protrusions equipped with 1 to 3 stiff cilia (Fig. 10c, inset) that protrude from an intraepithelial cluster of sensory cells. I have never found such sensory organs in buds and young individuals. Most remarkable is the ability of *L. antarctica* to shed and regenerate a calyx (Figs. 11; 12)—a regenerative capacity unique to this species amongst loxosomatids.

Measurements. *Weddell Sea specimens:* Total length: 1000 μm (595–1750 μm); length of calyx: 400 μm (380–636 μm); length of peduncle: 680 μm (240–1130 μm); width of calyx: 315 μm (208–414 μm); thickness of calyx: 317 μm (178–477 μm); diameter of peduncle: 133 μm (85–180 μm); diameter of peduncle in specimens with tapering peduncle: above 155 μm (127–180 μm), basally 104 μm (87–135 μm); number of tentacles: 12 (10–12). *Bransfield Strait specimens:* Total length: 1524 μm (636–2142 μm); length of calyx: 490 μm (318–625 μm); length of peduncle: 1074 μm (318–1525 μm); width of calyx: 280 μm (143–357 μm); thickness of calyx: 290 μm (159–318 μm); diameter of peduncle: 133 μm (95–220 μm); number of tentacles: 12 (10–12).

Habitat and distribution. In the Weddell Sea, *L. antarctica* has been found repeatedly at depths ranging from 100 to 400 m, growing in moderate numbers on the oral disc and the arms of the brittle star *Ophiurolepis gelida* (Fig. 8a), and, occasionally, in small numbers, on the dorsalmost fine setae (Fig. 10a, b) of the polychaete *Laetmonice producta* (Aphroditidae).

In the Bransfield Strait, *Loxosomella antarctica* is the most common loxosomatid, and grows on the same hosts; but it exhibits a conspicuous preference for the brittle star. Usually the ventral body surface and the arms of this host, as well as the dorsal side of the disc, are occupied by crowded populations of the loxosomatid at a density of about 4–6 individuals per mm^2 .

Beyond its Antarctic occurrence, the same species possibly has a second area of distribution in the Arctic Polar Sea. In the collections of the British Museum, a small sample of a loxosomatid (no. 31.7.3.1.70) was deposited which was collected from an *Eptizoanthus arborescens* colony near Bear Island (Greenland). Although the preservation state of these specimens is not the best, and they are identified by Mortensen himself as *Loxosomella antedonis*, it is evident that they lack bilateral sensory papillae, one of the striking species characters of the latter species (*cf.* p. #). Therefore, these Arctic specimens may also belong to *Loxosomella antarctica* Franzén, 1973. Especially with respect to the bipolar distribution of a number of entoprocts, a critical review of museum samples, as well as some new investigations in arctic waters, would be desirable.

Discussion of the species and the possibility of hybridization. Specimens from different hosts usually did not differ significantly, but samples from the Weddell Sea and

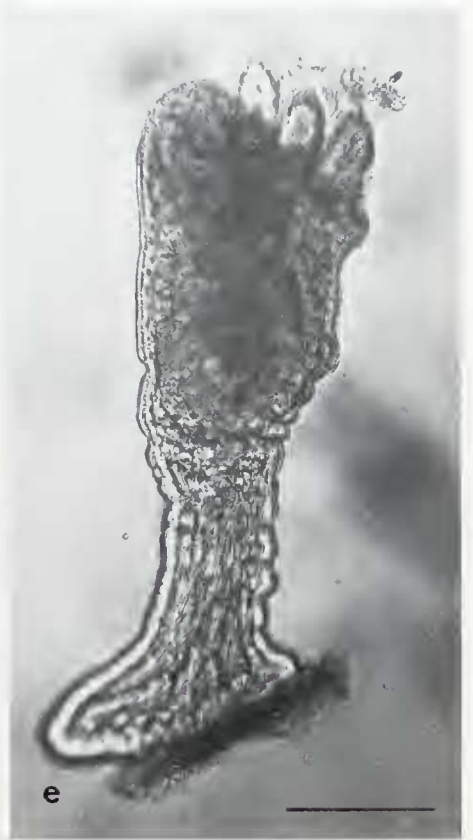
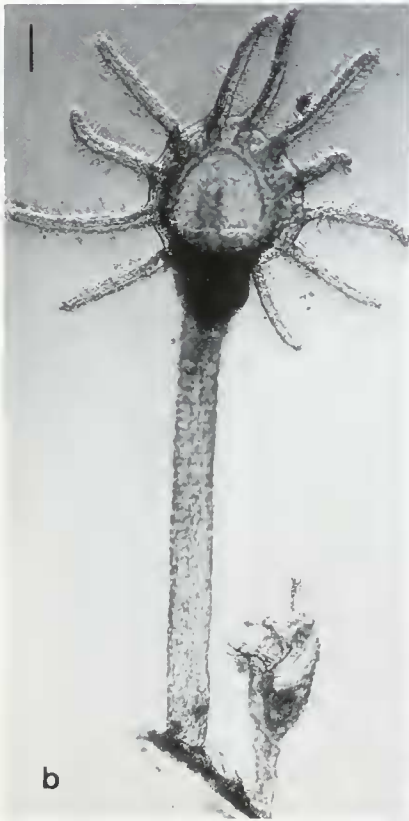
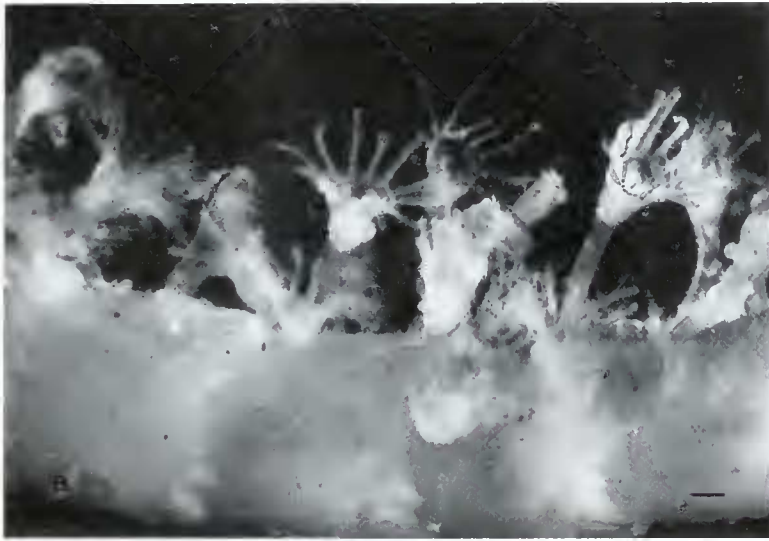


Figure 8. *Loxosomella antarctica*: a: Zooids settling tightly on an *Ophiurolepis* arm (scale 1 mm); b and c: living specimens in frontal and lateral view, respectively; d and e: young bud and newly detached bud; f: specimen from Franzén's type sample (bar 100 μ m).

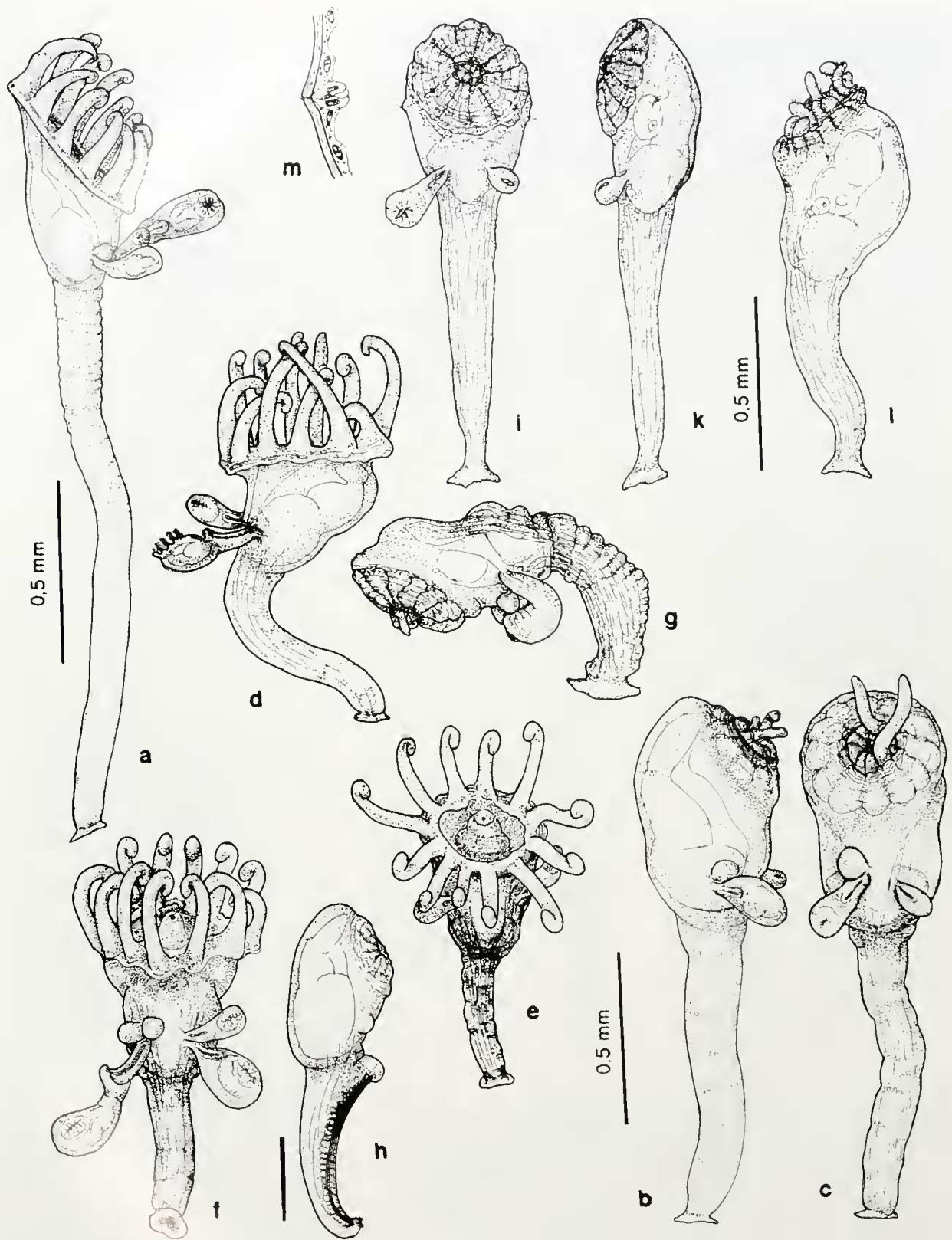


Figure 9. *Loxosomella antarctica*. a-c: expanded and contracted specimens from the Bransfield Strait: a: expanded specimen from *Ophiurolepis* (from life); b-c: preserved contracted specimens from *Laetmonice*; d-g: expanded and contracted specimens from the Weddell Sea (from life); d and e: from *Ophiurolepis*; f and g: from *Laetmonice*; h: newly detached bud; i-l: contracted Weddell Sea specimens from *Ophiurolepis* with tiny sensory spots (m) at either side.

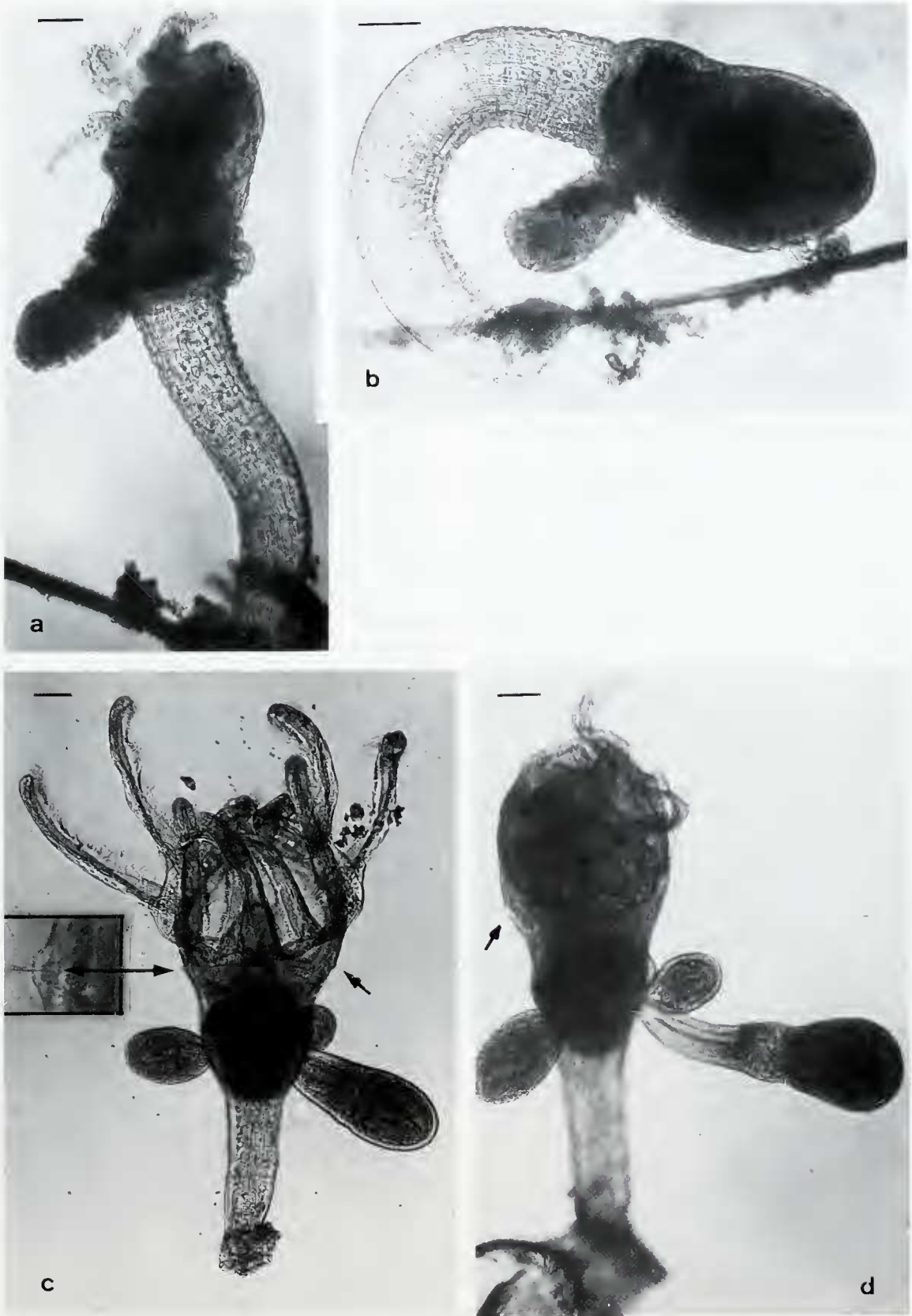


Figure 10. *Loxosomella antarctica*. a and b: Preserved Weddell Sea specimens from the setae of *Laetmonice* products; c and d: expanded and contracted Weddell Sea specimens from *Ophiurolepis gelida* with minute lateral sensory spots (arrows, inset) [bar 100 μ m].

the Bransfield Strait differ markedly in their average sizes. This may result from the conspicuous differences in the nutritional conditions in these regions; primary production, predominantly consisting of diatoms, is much richer in the Bransfield Strait than in the Weddell Sea.

A discontinuous presence of lateral sensory spots, which was observed in some rare cases in Weddell Sea specimens of *L. antarctica*, has been reported likewise for *Loxosomella claviformis* and *L. phascosomata* (Vogt, 1876); but the latter observations are not well established. Since all other characters of such Weddell Sea specimens with small lateral sensory papillae were within the normal range of variation of *L. antarctica*, and since such specimens were always found mixed with a majority of "normal" *antarctica*-zooids, they are considered to belong to the same species. Of course, such cases could also be produced by hybridization between *L. antarctica* and another species, such as *L. antedonis*, that is equipped with lateral sensory papillae.

At the one location in the Weddell Sea (stat. 16-369), where both of these species, *L. antarctica* and *L. antedonis*, occurred, they settled on different hosts and only in small numbers: *L. antarctica* on *Ophiurolepis* and *L. antedonis* on *Laetmonice*. Where *Loxosomella antarctica* occurred abundantly on both the ophiurid and (in smaller numbers) the polychaete, *L. antedonis* seemed to be generally absent. It was exactly under these conditions, amidst a majority of "normal" *Antarctica*-zooids, that zooids with tiny lateral sensory papillae were detected.

These findings are strongly suggestive of hybridization between these species, especially since, within the abundant *L. antarctica* populations of the Bransfield Strait where *L. antedonis* appeared to be generally lacking, no specimens with sensory papillae were detected. In fact, if hybridization between *Loxosomella antarctica* and *Loxosomella antedonis* is possible at all, then small disseminated populations of *L. antedonis* may well be absorbed by hybridization with the *antarctica* populations wherever the latter species is dominating. A sporadic appearance of *antedonis* characters in such hybridized populations must be expected. Both species can maintain themselves unhybridized only in macrobiotopes where they live as small populations that are spatially separated, e.g., on different hosts.

Regeneration. *Loxosomella antarctica* is the only solitary entoproct, for which the ability to regenerate a calyx has been demonstrated (Figs. 11; 12). Usually in Loxosomatidae the regenerative capacity is limited to the repair of single injured tentacles.

In abundantly growing populations of *Loxosomella antarctica* on *Ophiurolepis* from the Bransfield Strait, amidst great numbers of large active zooids, sporadic headless (no calyx) stalks were found. These stalks were still intact and were actively twisting and bending. At their headless apical end, they were sealed with a cuticular cap,

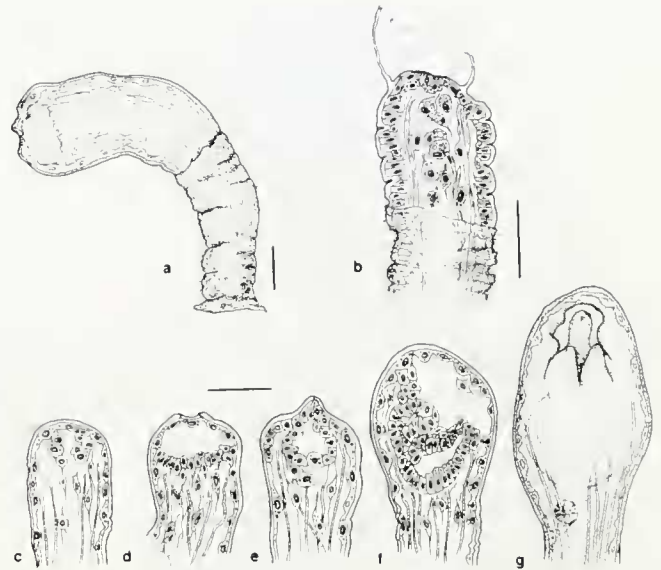


Figure 11. *Loxosomella antarctica*. stages of calyx regeneration. a: headless stalk in total view; b: apical region of a regenerating stalk with adhering remnants of the calyx cuticle; c-g: apical portions of several stalks in different regeneration stages: the beginning invagination and formation of the primary atrial vesicle (c, d), the initial gut formation (e), and differentiation of esophagus, stomach, intestine, and rectum (f), and (g) the atrial opening, newly broken through, and formation of the first oral tentacles (drawn after preserved samples).

and sometimes remnants of the cuticle of the shed calyx were still present. The basal portion of these peduncles is, in general, sharply delineated from the apical part by a different structure of the cuticle; basally, it is roughly wrinkled and coated by detritus particles, while apically it is thinner, smooth, and translucent (Figs. 11a, b; 12a, c). The same was observed in the stalks of many large active zooids—presumably an indication of successive growth periods.

Under the microscope, headless peduncles were observed in different stages of calyx regeneration. The earliest, least differentiated stages, have a thickened body wall epithelium throughout. At their distal ends they are contracted by the fibers of the well-developed longitudinal musculature, the remaining wound of the shed calyx being sealed off by a plug of epithelial cells and covered by a newly secreted cuticular cap (Figs. 11b-d; 12a, b). The innermost strands of the muscular layer are partly disintegrating, and the body cavity is filled with voluminous parenchyma cells containing many granules and vesicles, presumably storage proteins from phagocytized muscle cells. This picture resembles the muscular joints of barentsiid stalks when transforming into resting buds.

It can be inferred from the different stages observed that the subsequent regeneration of a calyx proceeds in the same way as in colonial entoprocts (Figs. 11b-g; 12b, d, e): (1) A primary atrial vesicle is formed by an apical invagination of body wall cells. (2) Gut and atrial floor

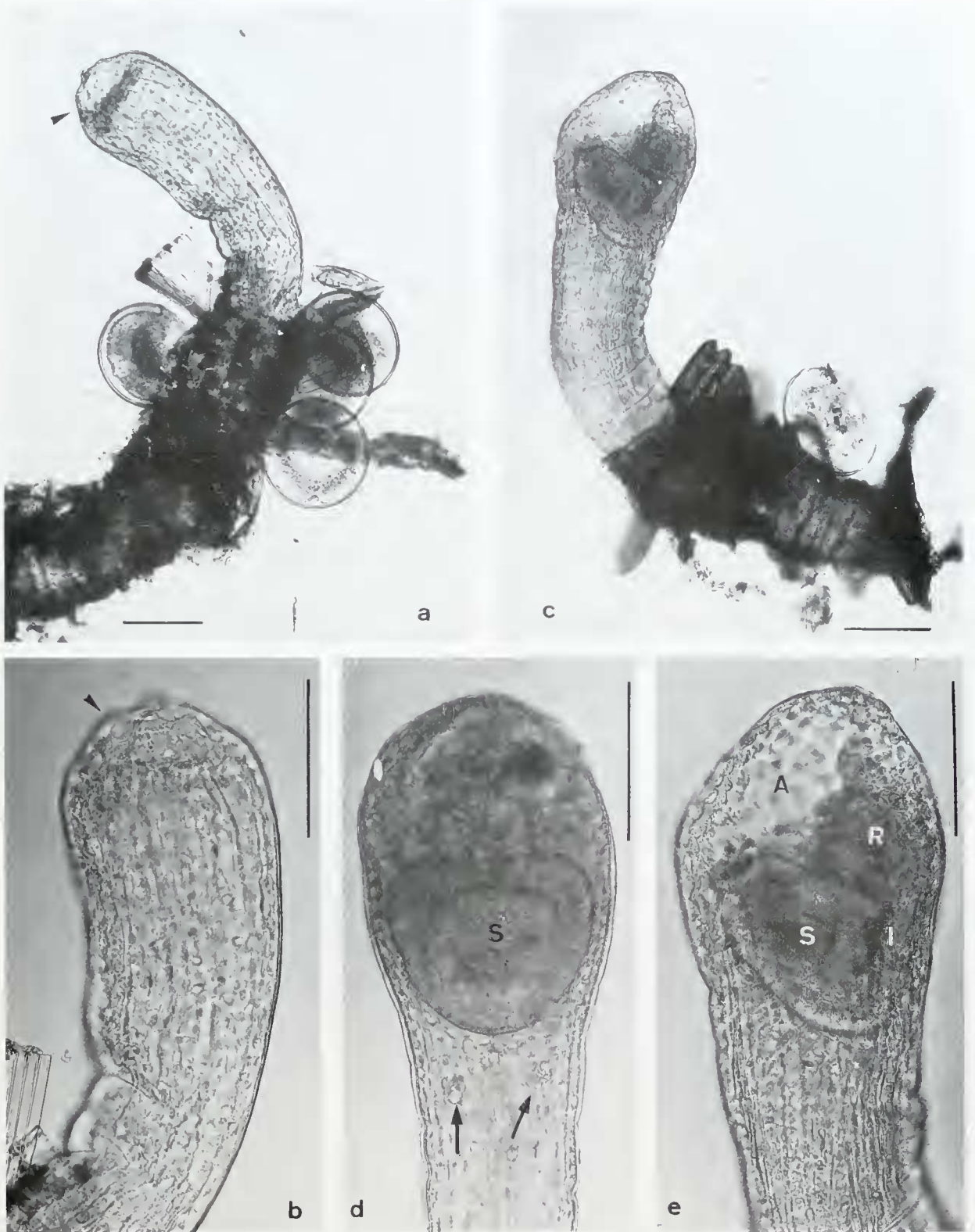


Figure 12. *Loxosomella antarctica*, calyx regenerating stalks: a and b: heavily cuticularized stalk with germinating tip; a primary atrial vesicle has formed (arrowhead); b–d: formation of the gut, the atrial opening not yet broken through; c and e: in lateral view; d: in frontal view; A - atrial cavity; I - intestine; R - "anlage" of the rectum; S - stomach; arrows - residual storage cells (bar 100 μm).

differentiate out of a basal cluster of the invaginated cells. (3) After the atrial opening has been broken through, the tentacles develop along the atrial rim beginning at the oral side.

The size of the headless peduncles, and their obviously successive stages of differentiation, preclude the possibility that they could merely be young metamorphosing specimens or old zooids in the course of degeneration. The former would be expected to be considerably smaller and in any case devoid of adhering apical cuticular remnants (Fig. 11b), whereas the atrium of the latter would never be completely closed (Figs. 11f; 12c–e).

Whether this calyx regeneration takes place as a consequence of external injury to the calyces, or is due to a periodic transformation of peduncles into resting buds under unfavorable environmental conditions, is presently indeterminable. All other loxosomatids examined in this respect under normal temperatures have an individual life span of hardly more than 6–10 weeks. During this time, depending on the nutritive supply, they continuously develop and release buds. Simultaneously, they pass through a short protandric male phase and a subsequent longer female phase. After having released about 10–20 larvae, the zooids degenerate. The larvae require at least about a week for metamorphosis.

The presence of apparently older basal portions and younger distal parts of the peduncles in larger zooids indicates a life span being extended over several growth periods. Such an increased ability to regenerate is obviously an adaptation to extremely short growth periods diminishing the chance of sexual reproduction. Under such circumstances an extension of the life span by an optional inactive resting phase is advantageous.

Loxosomella antedonis Mortensen 1911

Material. Collected by the author in the Weddell Sea at stations ANT VIII-5, 16-396 and 16-405 in depths of 300–400 m growing in moderate numbers on the dorsalmost fine setae of *Laetmonice producta* (Polychaeta, Aphroditidae).

The species was originally described by Mortensen (1911) from the northeast coast of Greenland, growing on the cirri of the feather star *Antedon proluxa*, and has been redescribed by Ryland and Austin (1960) from settlement panels off Swansea. I found it again in 1964, growing abundantly for a brief period on rocks and other solid substrates at the rocky shore around Helgoland. The species is very similar to young specimens of *Loxosomella antarctica*, but does not attain the length of the latter.

Description. The Antarctic specimens are 700 to maximally 1200 μm long, the slender, almost cylindrical peduncle being as long, or 1.5 times as long, as the calyx (Figs. 13a–d; 14a–e). The calyx, seen from the oral side, is inversely triangular in outline and slightly depressed in the oral-anal axis. In the expanded state, the calyx transforms gradually into the stalk. The large tentacular crown,

with 12–16 tentacles, when expanded, is conspicuously inclined to the oral side. In the contracted state the calyx is racket-shaped, flattened, with the lophophore facing frontally. The stomach is oval to inversely triangular with somewhat projecting lateral lobes. The peduncle, which bears longitudinal musculature that is not as strongly developed as in *L. antarctica*, terminates in an enlarged adhesive disc.

As a striking character, this species possesses at either side of the calyx, just beneath the lophophore and level with the stomach roof, a prominent, non-retractile sensory papilla, about 20–30 μm long, with a tuft of stiff bristles (Figs. 13b–d; 14b–d). Buds develop orolaterally in line with the upper half of the stomach. In contrast to those of most other loxosomatids, they have a very distinct T-shaped foot with a long anterior and posterior process, the peduncle inserting in the middle (Fig. 14e). Sometimes several fine sensory bristles are visible at the anterior tip of the foot.

Measurements. Total length: 900 μm (690–1450 μm); length of calyx: 420 μm (336–548 μm); length of peduncle: 508 μm (361–651 μm); width of calyx: 265 μm (233–308 μm); thickness of calyx: 185 μm (169–189 μm); diameter of peduncle: 107 μm (93–117 μm); number of tentacles: 14–16; length of sensory papillae: 20–30 μm .

Habitat and distribution. In Antarctic waters, the species has been found only in the Weddell Sea, growing exclusively on *Laetmonice producta*. West of the Antarctic Peninsula it seems to be absent. The actual distribution of *Loxosomella antedonis* probably consists of the arctic and subarctic region, where it settles on various living as well as dead substrates, showing no host specificity.

Additional remarks to the species. The Weddell Sea specimens agree quite well with Mortensen's original description of *Loxosomella antedonis*, as well as with Ryland's and my own specimens from the Irish- and the North Sea. Though the original type specimens have been lost, the conspicuous lateral sensory organs, mentioned and figured by Mortensen, present a striking species character. A sample of specimens without such papillae, deposited in the British Museum (*cf.* p. #) and identified by the late Mortensen as *Loxosmella antedonis*, is definitely different from this species.

Loxosomella compressa Nielsen and Ryland 1961

Synonym. *Loxosomella compressa* var. *antarctica* Franzén, 1973.

Material. This species was abundant at depths from 100 to 400 m at almost all stations in the Weddell Sea, but was absent at depths greater than 500 m. In the Bransfield Strait it was found at one single location (Met. XI-4/39-90), at a depth of 160 m, generally growing on the dorsal setae of a great variety of polynoid polychaetes.

Loxosomella compressa, first described by Nielsen and Ryland from the Norwegian coast, growing on the notopodial setae of several polynoids, turned out to be the most common entoproct in the Weddell Sea. In this area, it apparently prefers the same hosts as in its northern area of distribution.

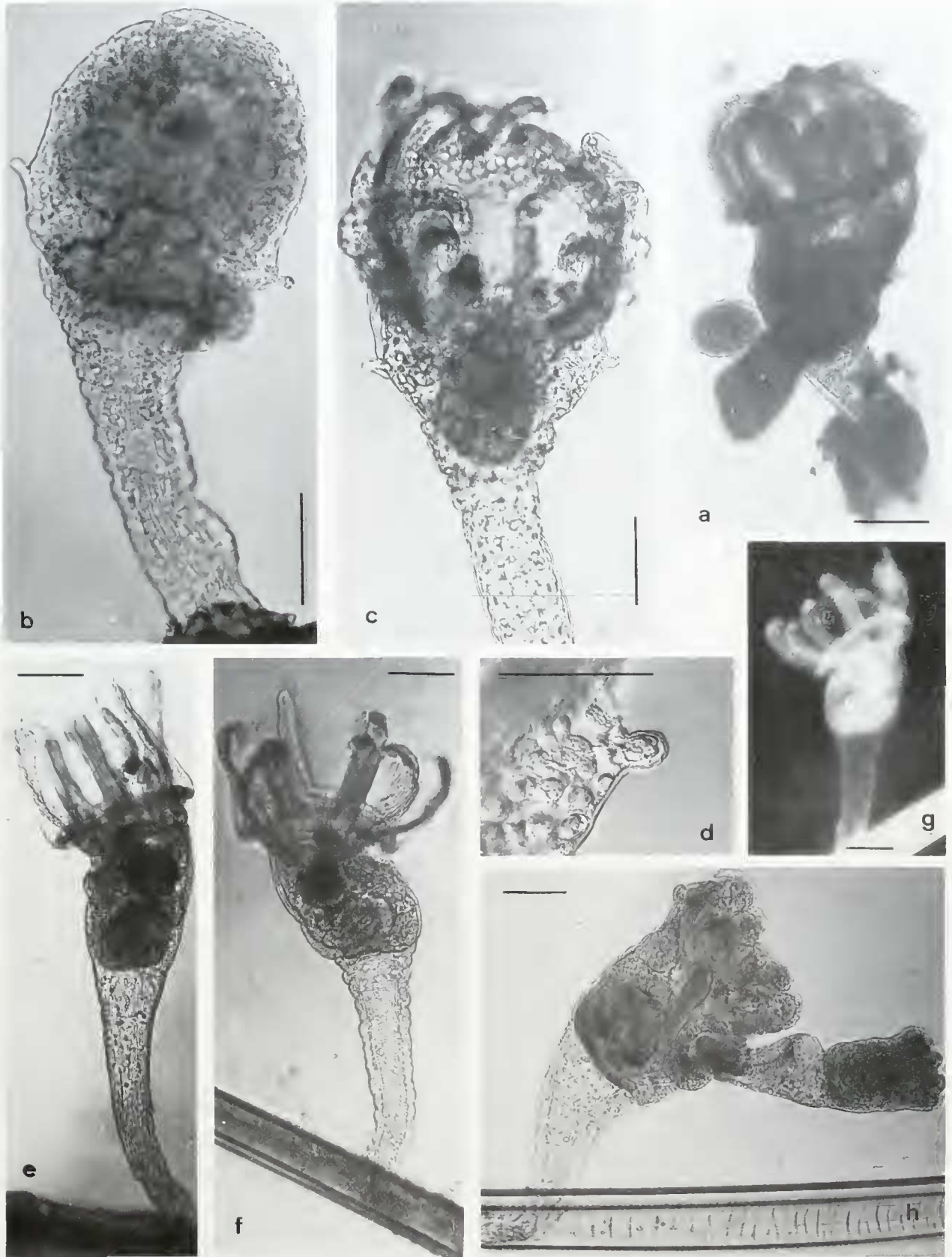


Figure 13. a–d: *Loxosomella antedomis* from the Weddell Sea. a: living expanded specimen; b–c: preserved specimens, the large sensory papillae (d) are conspicuously visible; e–h: *Loxosomella compressa*: preserved expanded specimens (e–f) and living specimen (g) in natural posture on polynoidan setae; h: preserved specimen with large bud (bar 100 μm).

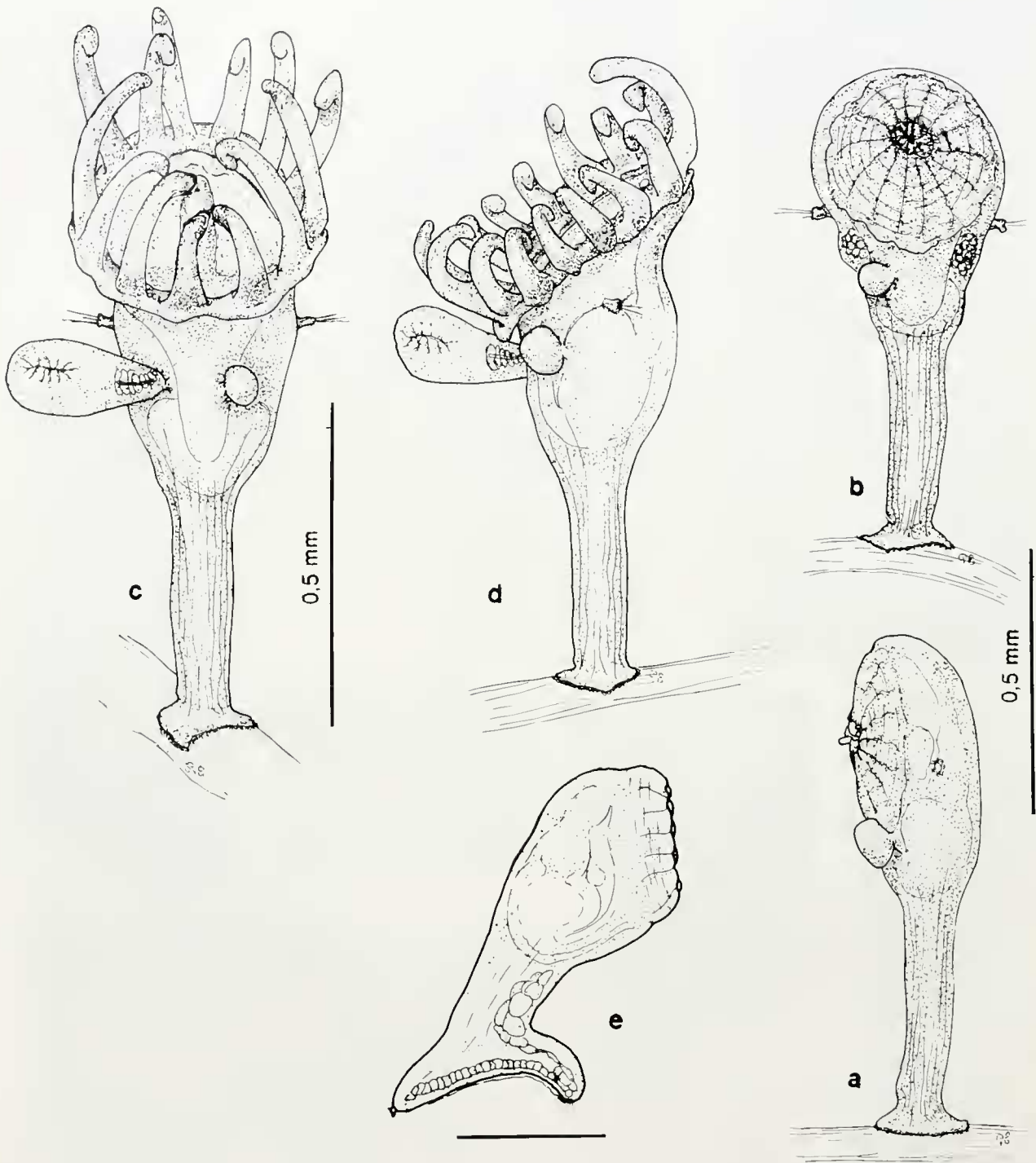


Figure 14. *Loxosomella antedonis* from the Weddell Sea. a–b: contracted specimens from the Weddell Sea (preserved material); c–d: expanded specimens from life, the large sensory papillae being conspicuous in all specimens; e: newly detached bud with its typical T-shaped foot.

Description. A medium size species, easily recognized by its peculiar laterally depressed calyx and by the formation of its buds almost medially, level with the stomach roof, and perched on a console-like protuberance of the oral calyx wall.

The total length of mature, budding Weddell Sea specimens varied between 500 and 750 μm . Seen from the side the calyx is goblet-shaped, with a kind of "paunch" below the budding zone (Figs. 13e–h; 15b–e). With no conspicuous demarcation, it transforms into the slender

stalk, which ends in a small attachment disc. Seen from the frontal side, the calyx is slim, and of the same diameter as the upper part of the peduncle which tapers downwards. The comparably large lophophore with 8 tentacles faces nearly straight up, both in the expanded and contracted state.

The stomach is large and globular. The buds, rarely more than one at either side, are normally oriented in an upright position, rather than hanging downwards (Figs. 13h; 15c). They have a very short stalk and a well-developed, posteriorly extended foot, with a glandular groove along its whole length (Fig. 15i). The latter is lined with large glandular cells. The main portion of the gland is situated just below the stomach. Gonads were observed in detached animals only. Smaller specimens contained both immature testes as well as young ovaries, while larger specimens exclusively contained mature ovaries and brood pouches with embryos and larvae in different developmental stages.

Measurements Total length: 640 μm (540–750 μm) (Nielsen: 500 μm , max. 700 μm ; Franzén: 870 μm); length of calyx: 290 μm (240–348 μm) (Nielsen: 178 μm ; Franzén: 457 μm); length of stalk: 360 μm (300–460 μm) (Nielsen: 267 μm ; Franzén: 411 μm); width of calyx: 183 μm (180–190 μm) (Nielsen: 78 μm ; Franzén: 195 μm); thickness of calyx: 215 μm (176–246 μm) (Nielsen: 120 μm ; Franzén: 257 μm); diameter of peduncle: above 137 μm (101–168 μm), below: 60 μm (53–75 μm); number of tentacles: 8 (Nielsen: 8–9; Franzén: 8).

Habitat and distribution. *Loxosomella compressa* was found exclusively perched on the notopodial setae of a broad spectrum of Polynoidae (Fig. 15a). It was never found on other hosts, although about a thousand specimens of a great number of other polychaete species occurring in the same locations were searched for epizoans. Predominantly smaller polynoids (4–10 cm) are chosen as hosts, and species with short and thick notopodial setae covered by the elytrae are preferred; the loxosomellae are attached at the setal bases. On average, 2–4 individuals were found per parapodium, but at several locations offering exceptional nutritional conditions, up to 8 individuals per parapodium were counted. Under such conditions of extreme scarcity of unoccupied substrate, other polynoid species with dense bunches of thinner notopodial setae, or with dorsal setae not covered by the elytrae, e.g., *Hermadion ferox*, served as hosts for *Loxosomella compressa*.

In culture experiments aboard ship, *L. compressa* could be kept actively budding for about 3–4 weeks. In aquaria containing some polynoid hosts with their epizoans, newly detached buds were found to settle and become themselves actively budding on diverse solid substrates, such as stones and small settlement panels.

In the Weddell Sea, *Loxosomella compressa* is the most common entoproct occurring at depths from 100 and 500 m all along the Antarctic shelf from its northeastern edge to Kap Fiske, at the base of the Antarctic Peninsula. West of the peninsula, in contrast, this species seems to be rare,

having been found there at only a single location north of Tower Island (stat. 39-90) and in very small numbers. Moreover, this species is also distributed in the Indic sector of the Antarctic Ocean. I detected it in several samples taken by Russian and Soviet Antarctic expeditions: in 1903 at the Alasheyev Bight, off today's Soviet station Molodeshnaya, in 1956 at the Budd Coast, in 1957 off the Lars Kristensen Coast, and in 1965 at the Tokarjev Island, growing on *Harmothoe molluscum* and *H. gourdoni*.

Franzén reports this species from the subantarctic region as occurring abundantly in samples taken in 1902 at the northernmost tip of the Antarctic Peninsula (Seymour Island), as well as from the Falkland Islands (Islas Malvinas), and from South Georgia where it reaches a size of 800–900 μm .

In the northern hemisphere, *Loxosomella compressa* is common in the whole arctic and subarctic regions, where it is reported to occur abundantly on several polynoids (*Lagisca extenuata*, *Gattyana cirrhosa*, *Acanthiolepis asperrima*, and *Harmothoe haliaeti*). It also occurs along the English and Norwegian coasts, in the Skagerrak and Kattegatt (Nielsen and Ryland, 1961; Nielsen, 1964a-b; Eggleston, 1965, 1969; Eggleston and Bull, 1966; Jones, 1963), as well as all along the shelf to the Arctic Polar Sea, from the Barents to the Kara Sea, living on the polynoids *Harmothoe imbricata*, *Antinoella badia*, *A. sarsi* and *Eunoe hartmannae* (Emschermann, unpub.). In the entire mid-Atlantic, as well as in the Pacific, this species seems to be absent.

Loxosomella varians Nielsen 1964

Synonym. *Loxosomella brachystipes* Franzén 1973.

Material. Collected in the Weddell Sea by the author (stations ANT VIII-5, 16-396 and 16-454), at depths from 270 to 400 m on stony bottoms and in the Bransfield Strait by Dr. U. Wirth (stations Met.XI-4, stat. 8-90, 39-90, and 96-90) at depths from 100 to 150 m on muddy grounds, this species grew in moderate numbers on the gills (Fig. 17a) of *Aglaophamus foliosus* (Polychaeta, Nephthyidae). The species was originally described by Nielsen as common in the North as well as in the Baltic Sea living on the gills of several nephthyid polychaetes.

Description. The specimens from the Weddell Sea, as well as from the Bransfield Strait, are in good agreement with Nielsen's description: a small variable species of about 300–500 μm total length, with a bulgy goblet-shaped calyx on an almost short, sturdy peduncle, distinctly marked off from the calyx, and terminating in a more or less extended foot plate of variable form (Figs. 16; 17; 18a–h).

The calyx is laterally depressed; the comparatively large tentacular crown with its 8 slender tentacles faces upwards, slightly inclined to the oral side. The stomach is large and globular. Buds are formed at the oral side in two adjacent paramedial areas in line with the roof of the stomach. Under favorable conditions, they can build up a crowded

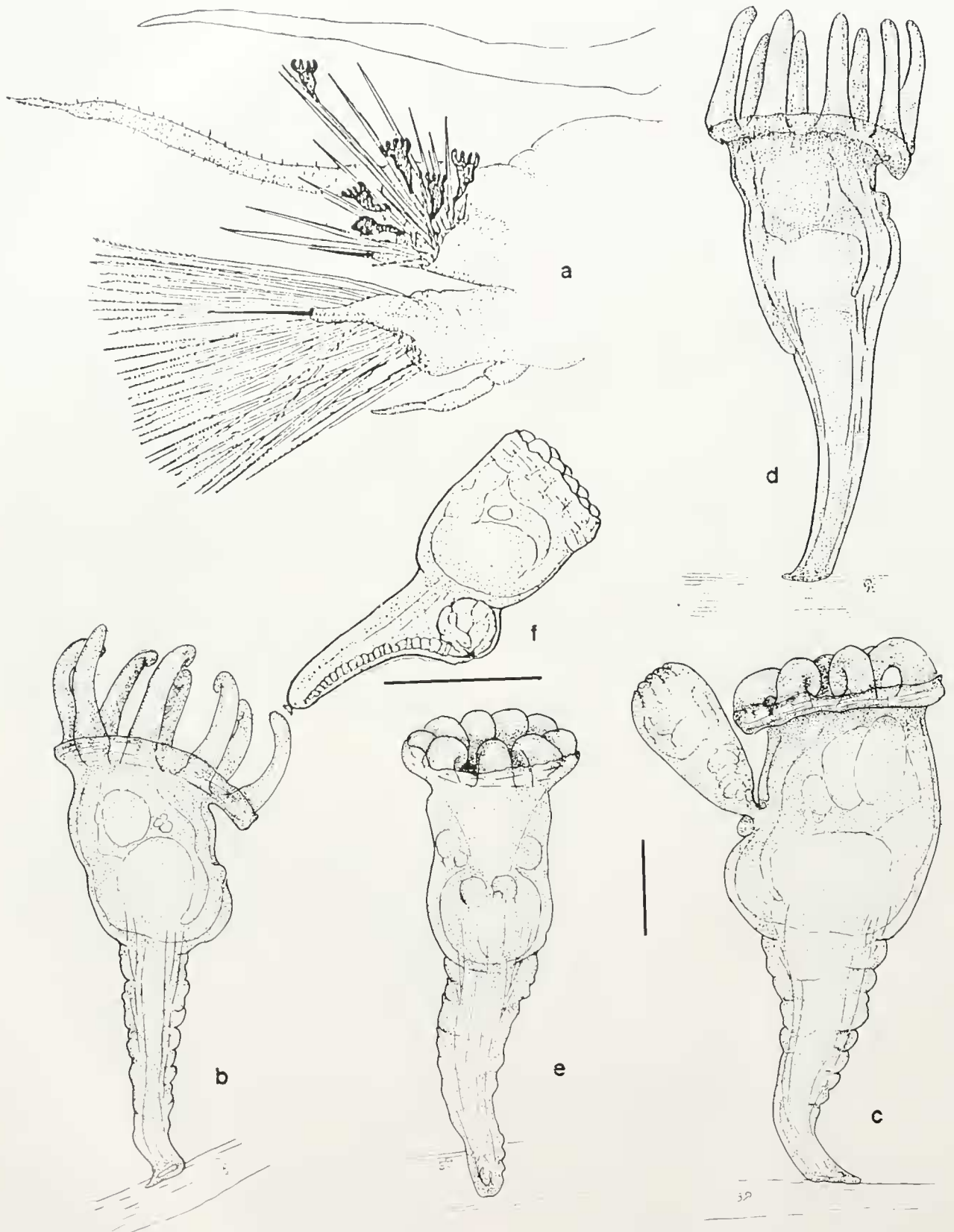


Figure 15. *Loxosomella compressa*. a: polynoid parapodium with loxosomatid specimens on the notopodial setae; b-c: living expanded and contracted specimens in lateral and frontal view; d: preserved specimen in expanded state, seen from lateral; f: newly detached bud.

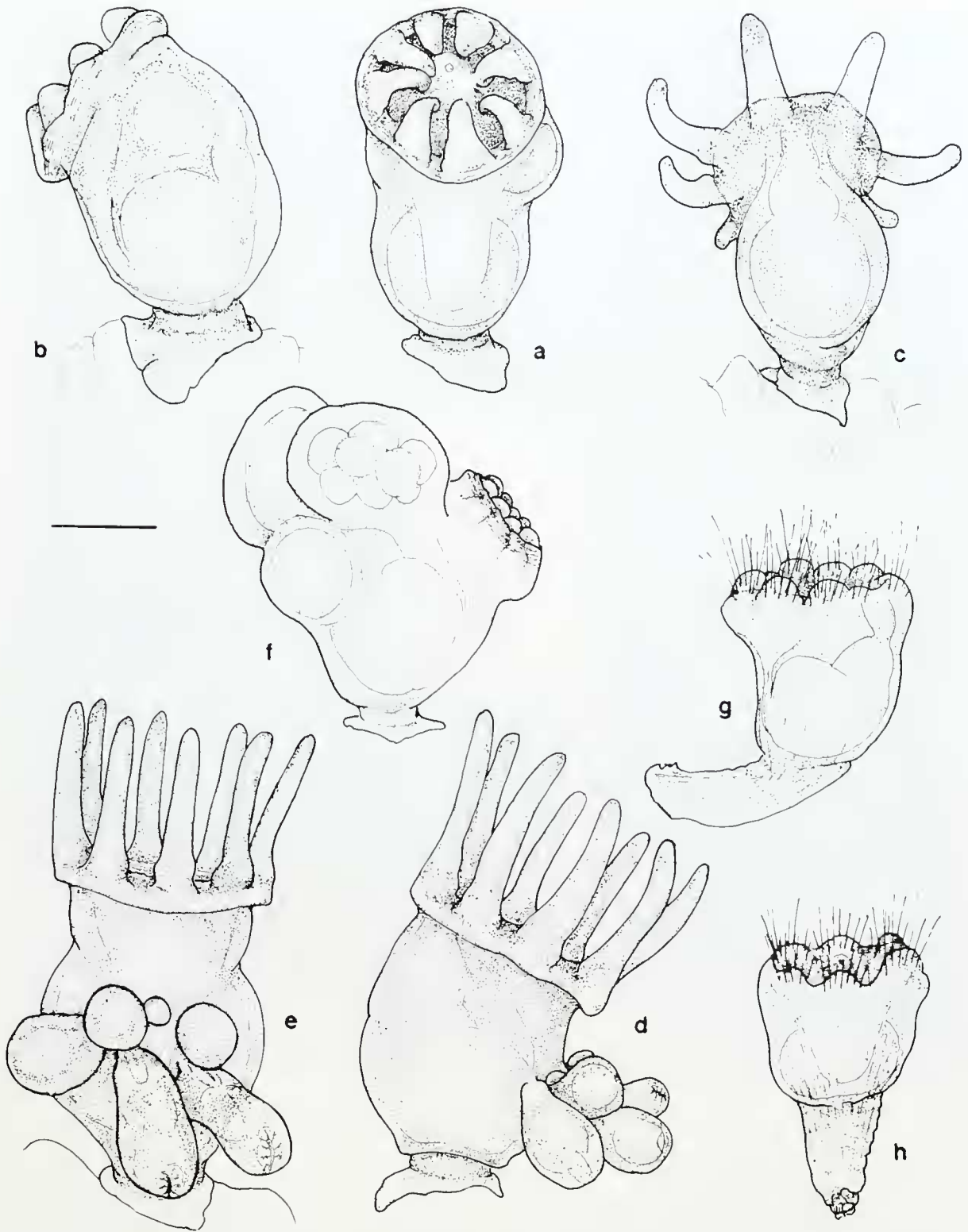


Figure 16. *Loxosomella varians*. a-c: two more or less expanded Weddell Sea specimens in frontal, lateral, and abfrontal view, respectively; d-e: specimen from the Bransfield Strait with a total of six buds in two paramedian clusters, in lateral and frontal view, respectively; f: preserved specimen with larvae in the brood pouches at either side; g-h: abnormal newly detached buds.

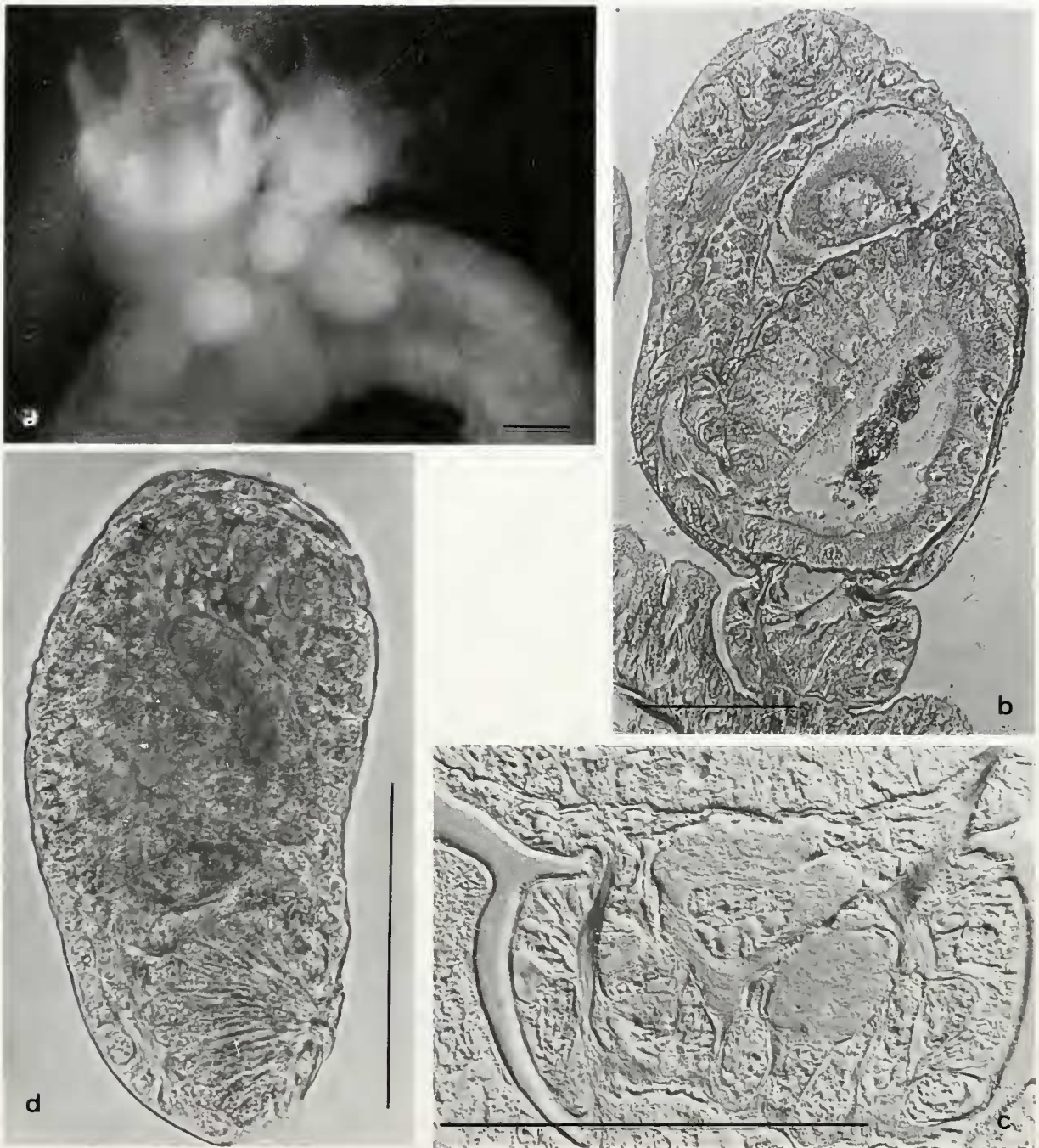


Figure 17. *Loxosomella varians* from the Weddell Sea, specimen with a cluster of 7 buds of different age on a parapodial cirrus of its host, *Aglaophamus foliosus*: b-c: Type specimen of *Loxosomella brachystipes* Franzén (c: foot of b enlarged); d: young bud from Franzén's type specimens with the clearly visible foot-gland (bar 100 μ m).

cluster of eight and more buds which appear to originate from a single medial budding area (Figs. 16e, d; 17a).

The foot-gland in young buds forms a small groove; in older ones a slit-like invagination is bordered by densely arranged, elongated, club-shaped gland cells (Figs. 17d; 18i-m). In the adult foot plate, parts of the adhesive gland usually persist as a row of marginal large cells around the

rim of the basal disc. Sometimes an additional plug of epithelial cells is formed in the middle of the foot (Fig. 18e, o-p).

Most specimens contained immature and mature ovaries, whereas testes were seen only in older undetached buds. In animals bearing larger embryos or larvae, the aboral calyx wall at either side, just below the tentacular

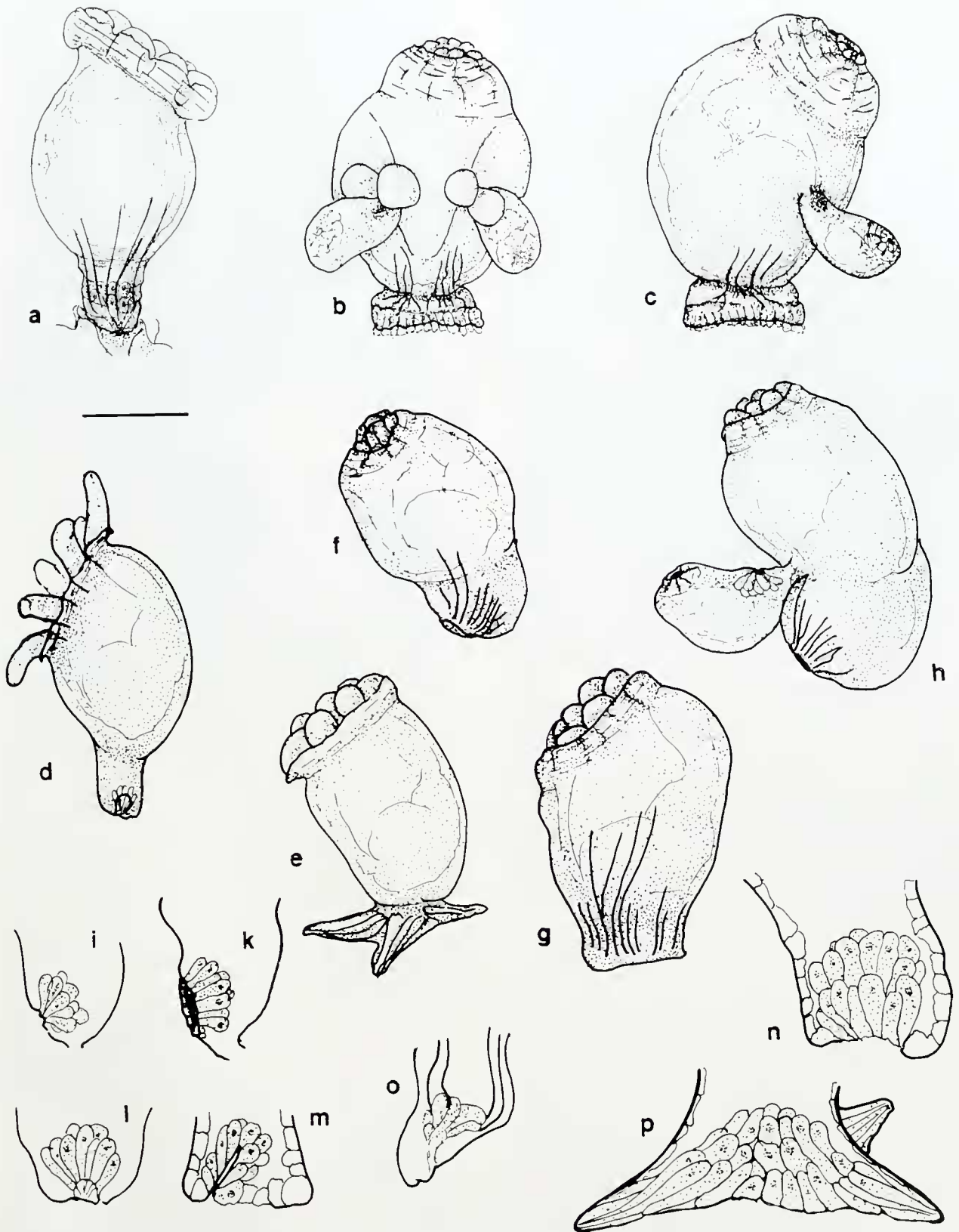


Figure 18. *Loxosomella varians*. Comparison of a Bransfield Strait specimen (a) with type specimens of *Loxosomella brachystipes* Franzén (b-c) and paratypes of *L. varians* Nielsen from the Kattegat (d-h); i-n: shape of the foot-gland in buds (i from Franzén's, k from Nielsen's samples) and in newly detached specimens (l-n); o-p: adhesive plates in adult specimens from Nielsen's paratype material.

crown, bulged out due to the enlarged brood pouches, like a clumsy rucksack almost equal in size to the entire normal calyx (Fig. 16f).

Measurements. Total length: 370 μm (300–485 μm) (Nielsen 392 μm ; Franzén: 426 μm); Length of calyx: 305 μm (175–325 μm) (Nielsen: 285 μm ; Franzén: 375 μm); length of stalk: 65 μm (32–111 μm) (Nielsen: 107 μm ; Franzén: 51 μm); width of calyx: 223 μm (191–254 μm) (Nielsen: 200 μm ; Franzén: 292 μm); thickness of calyx: 290 μm (175–461 μm) (Nielsen: 205 μm ; Franzén: 332 μm); number of tentacles: 8 (Nielsen: 8; Franzén: 8); maximal number of buds: 8 (Nielsen: 15).

Additional remarks on the variability of this species.

Although highly variable, especially with respect to the length of the stalk and shape of the foot plate, the species is well-defined by its general body shape, the crowded buds, and the paramedial budding areas, as well as by the small groove-like foot-gland in the buds.

In 1973, Franzén described a new loxosomatid found in small numbers on the gills of *Aglaophamus virginis* (Polychaeta, Nephthyidae), from old samples collected northeast of South Georgia during the 1902 Swedish Antarctic expedition; he named it *Loxosomella brachystipes* (Figs. 17b, c; 18b, c). This species, in most instances, looks like *Loxosomella varians*, but according to Franzén, the shape of the foot is markedly different in these two forms. However, judging from the present samples, both of these forms must be considered identical, because they cover the whole range from *L. varians*- to *L. brachystipes*-type specimens. So, in agreement with Franzén, they must be considered synonymous (see Fig. 18 regarding the variability of this species).

Habitat and distribution. *Loxosomella varians* has been found living on the gills of a broad spectrum of nephthydid polychaetes, never on hosts belonging to other polychaete families. In the Atlantic sector of the subantarctic and Antarctic Sea, this species is widespread from South Georgia, south to the eastern Weddell Sea, and along the western coast of the Antarctic Peninsula. In the northern hemisphere, *Loxosomella varians* is reportedly common in the North and Baltic Seas, but it seems to be absent from the midatlantic region and the Pacific Ocean.

Barentsia discreta (Busk 1886)

Synonyms. *Ascopodaria discreta* Busk, 1886; Kluge, 1946; Thornely, 1905; *Ascopodaria macropus* Ehlers, 1890; Robertson, 1900; *Barentsia antarctica* Johnston and Angel, 1940; *Barentsia discreta* Annandale, 1915; O'Donoghue, 1920; Emschermann, 1985; Franzén, 1973; Harmer, 1915; Hutchins, 1945; Johnston and Angel 1940; Kirkpatrick 1888; Konno 1971; Marcus, 1922, 1937, 1953; Maturo, 1957; Mukai and Makioka, 1980; Okada and Mawatari, 1938; Osburn, 1912, 1914, 1932, 1944, 1953; Rogick, 1956; Toriumi, 1949, 1951; Vigeland, 1937/38; Waters, 1904; *Barentsia gracilis* Norman, 1907/10; *Barentsia intermedia* Johnston and Angel, 1940; *Barentsia misakiensis* Oka, 1895; *Barentsia tumida* Verrill, 1900.

Material. In the Weddell Sea, small colonies were found on diverse solid substrates from three locations (ANT VIII-5/16-396 and 16-456, and additionally in older samples collected at 76° 36.0'S; 30° 33.3'W). In the Bransfield Strait, samples were found at all stations, except 66-90, in a depth range of 80 to 400 m.

Description. Living colonies of *Barentsia discreta* (Fig. 19) can immediately be recognized macroscopically by the vivid bending and twisting movements of the tall, 4–6 mm-long zooids arising from large, cylindrical, and delicately annulated basal sockets. The slender and predominantly rigid stalk bears a broad, cup-shaped calyx with the circle of 20–24 long tentacles facing straight up. The rigid part of the stalk, depending on the growth conditions, may be the same diameter over its entire length, or may widen slightly distally. Its smooth, yellowish to brownish cuticle is usually perforated by more or less numerous, minute, pore-like openings of subcuticular epithelial organs; the latter are presumably ion regulating cells homologous to protonephridia (Emschermann, 1972, 1982). As is normal for Barentsiidae, the rigid portion of the stalk distally, just below the calyx, turns into a short muscular segment with a wrinkled flexible cuticle. This distal

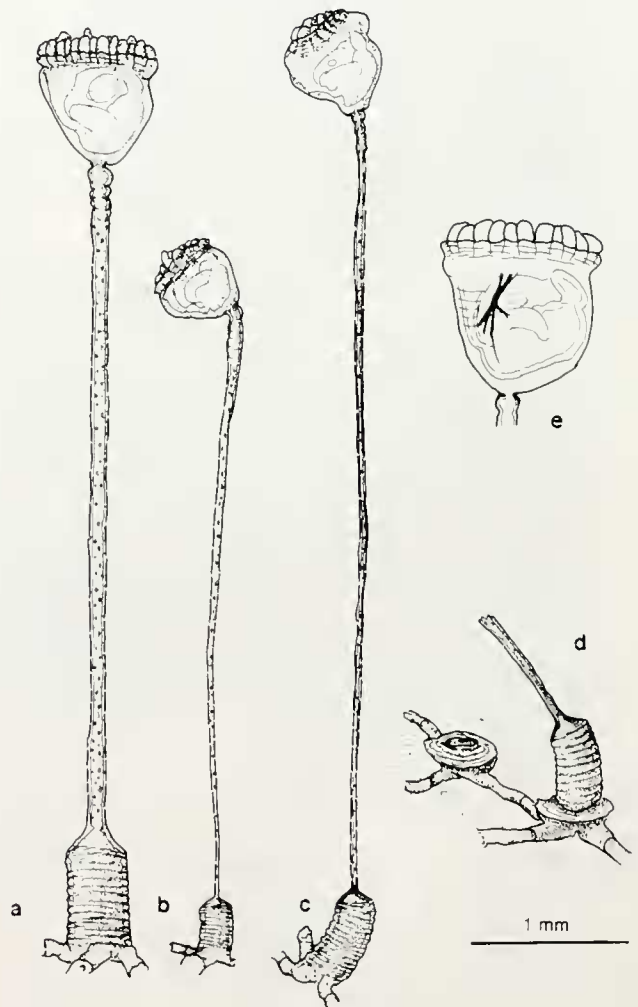


Figure 19. *Barentsia discreta*. a–c: three zooids from the Bransfield Strait (a) and the Weddell Sea (b, c); d: basal socket with a disc-shaped resting bud below it (part of a colony from the Bransfield Strait); e: calyx with the characteristic atrial retractor muscle indicated.

stalk segment has the capacity for calyx regeneration. Under favorable growth conditions, after degeneration of a calyx, and before its regeneration, the muscular section may give rise to a second stalk segment, consisting in turn of a proximal stiff and a distal muscular portion. The primary muscular swelling in such a case persists as an intercalating muscular joint, separated from the next segment by a cuticular hemiseptum. A stack of 8 to 10 star-shaped transverse muscle cells ("star cells" Emschermann, 1969) forms a sort of diaphragm between stalk and calyx.

In older well-fed colonies, a cup-shaped secondary inflation can develop below the bases of the zooid muscular sockets (Fig. 19d); the inflation is filled with storage cells and is separated by a diaphragm from the zooid base. These basal inflations function as resting buds, being resistant to mechanical damage, as well as temperatures up to 25°C, and even against being embedded in ice or drying for at least a week. They give rise to new zooids after the primary ones have been damaged or have died.

The structure of the calyx musculature, in particular the shape of the paired atrial retractor muscles, is a useful and reliable species character (Fig. 19e), as in most Barentsiidae (Emschermann, unpub.). In *Barentsia discreta*, three fine muscular strands on either side originate from the atrial floor just behind the mouth. Running downwards, in line with the roof of the stomach, they unite to form a short muscular ribbon. This in turn bifurcates again into an anterior and a posterior branch, each splitting into 2 to 5 fine single fibers, which insert in the lateral calyx walls at either side of esophageal entrance into the stomach. These atrial retractors can best be visualized in contracted calyces with polarized light or Nomarski interference contrast.

In the Antarctic samples, sexually mature zooids with both ovaries and, more rarely, testes were found.

Measurements. Total length of zooids: 4–6 mm; length of muscular base: 0.8–1.1 mm; diameter of muscular base: 0.3–0.44 mm; length of the distal muscular portion of the stalk: 180–330 μ m; length of calyx: 580–700 μ m; number of tentacles: 20–24.

Additional remarks about the species. *Barentsia discreta* has been found worldwide, the size of the zooids varying considerably, not only from location to location, but also under different nutritive conditions at the same locality. The cylindrical (but never barrel-shaped), annulated muscular base, the stalk-rigid over nearly its entire length with only a short muscular portion below the cup-shaped calyx, and the typical structure of the atrial retractor muscles are reliable, if only morphological, species characters. In colonies of different origin (California, Florida, and the Mediterranean Sea) cultured in the laboratory under the same conditions, no significant morphological differences between the specimens of different origin were found (Emschermann, unpub.). Their range of variation falls within that of the Antarctic material. Interbreeding between different populations can be observed in culture to

the extent that the experimental populations are able to be active and become sexually mature under the same environmental conditions. In their physiological tolerance to environmental conditions, such as temperature, populations from different parts of the world can differ markedly. An Antarctic colony in my laboratory cultures did not remain active at temperatures above 4–5°C, but in an inactive state, it tolerated temperatures up to 15°C for several weeks. On the other hand, populations from temperate climates are able to tolerate low temperatures nearly to freezing, but they do not develop gonads under these conditions. To date, no long term attempts to gradually adapt colonies of different origin to lower or higher temperatures, have been carried out).

Therefore the genetic exchange between the Antarctic populations and others may be considerably reduced, but not interrupted. Their morphological conformity can be seen as an indication that they are not genetically isolated, and the populations of *Barentsia discreta* reported worldwide may be thought of as belonging to the same species (*cf.* Franzén, 1973, p. 185).

Habitat and distribution. In the Weddell Sea, especially in the eastern part, *Barentsia discreta* is found regularly, but never abundantly, at depths between 200 and 400 m. This species grows on every solid substrate, preferably on primary or secondary hard bottoms, basally on the stems of erect hydrozoan and bryozoan colonies, as well as on stones, shells, and even on brittle stars. But in the Bransfield Strait, the species occurred abundantly everywhere at depths from 80 to 500 m, presumably because of the more favorable nutrient conditions throughout the year in this region.

In general, this species is distributed worldwide, missing only from the Atlantic-subarctic European coasts. Furthermore, it is reported circumantarctically, along the shelves of Antarctica itself and the subantarctic islands (Busk, 1886; Franzén, 1973; Johnston and Angel, 1940; Rogick, 1956; Vigeland, 1937/38; Waters, 1904). Along the South and North American coasts, its distribution extends, on the Atlantic side, from Tierra del Fuego, along the Argentinian and Brazilian coasts (Marcus, 1937, 1953), the Caribbean Sea (Osburn, 1914, 1940; Emschermann, unpub.), and Florida (Nielsen, pers. comm.), up to the Massachusetts Bay in the north (Hutchins, 1945; Maturo, 1957; Osburn, 1912, 1932, 1944); on the Pacific side, it extends from southern Chile and along the coast of Central America (Osburn, 1953), to California (Robertson, 1900; Emschermann, 1985).

In the Atlantic region, and along the European coasts, the species is reported from the Bermuda Islands (Verrill, 1900; Maturo and Schopf, 1968), from Madeira (Norman, 1907/10; Emschermann, unpub.) and the Azores (Emschermann, unpub.), and from the Mediterranean Sea (Ehlers, 1890; Zirpolo, 1927; Emschermann, unpub.).

In the Indo-Pacific region, *Barentsia discreta* seems to be common everywhere, from South Africa (O'Donoghue, 1920), the Indian Ocean (Annandale, 1915; Harmer, 1899; Kirkpatrick, 1888; Thornely, 1905) and South-Pacific (Marcus, 1922), to the Chinese- and Japanese Sea (Konno, 1971; Oka, 1895; Okada and Mawatari, 1938; Toriumi, 1949, 1951; Yamada, 1956). Finally the species was reported by Kluge (1946) from the Laptev Sea (Siberian Polar Sea).

Some General Concluding Considerations

Besides representing merely a faunistical survey, four particular aspects of the above results are of special interest: (1) the detection of nematocyst-like organs in an entoproct; (2) the ability of a loxosomatid to regenerate its calyx; (3) some additional observations on the nature of host preference or host specificity of the Loxosomatidae; and (4) the bipolar occurrence of several *Loxosomella* species.

(1) The detection of *extruding organs* in an entoproct raises questions about their comparative morphological importance and their phylogenetic significance. Comparable, usually unicellular, extrusive glandular organs, which produce clearly structured secretions, have been described in quite a number of invertebrate phyla, in addition to coelenterates: in Platyhelminthes (only in Turbellaria; Reisinger and Kelbertz, 1964; Smith *et al.*, 1982), Gastrotricha (Rieger *et al.*, 1974), Nemertini (Jennings and Gibson, 1969), Gnathostomulida (Rieger and Meinitz, 1977), and the Archiannelida among the annelids (Martin, 1978). Except in the Cnidaria, Ctenophora, and Turbellaria, these extrusion organs do not represent typical characters of the above animal taxa, but occur in isolation in one or another species. Only in Cnidaria and Ctenophora do the extrusive organs eject harpoonlike, poisonous or sticky threads. In all of the other above taxa the extrusive gland cells produce rod-like mucous secretions of the rhabdite type. The probably syncytial plurinuclear extrusive capsules of *Loxosomella brochobola* seem, at present, to be unique in the animal kingdom and to differ remarkably, in development, structure, and extrusion mechanism, from comparable organs in other groups. Thus they must be considered as an isolated apomorphic character of this particular entoproct species, rather than a character of phylogenetic significance. Probably they are derived, in a highly specialized form, from conspicuous uni- or pluricellular mucous glands of unknown function, which occur in a number of loxosomatids around the margin of the tentacular crown.

(2) The *ability to regenerate calyces* in *Loxosomella antarctica* is unusual for solitary entoprocts. Distinct from *Loxokalyptus socialis* (Emschermann, 1972)—another entoproct species with an enhanced regenerative capacity, and in which the budding zone has shifted from the calyx

wall down to the stalk as a first evolutionary step towards the colonial growth pattern—normal asexual budding in *Loxosomella antarctica* proceeds as usual in two paired budding areas on the oral wall of the calyx. Therefore, the enhanced regeneration capacity of the distalmost tip of the stalk epithelium in *L. antarctica* (Figs. 11; 12) is an isolated secondary adaptation to the conditions of Antarctic life. This is important to the biology of entoprocts, but is without phylogenetic significance.

(3) A marked *host specificity* is thought by several authors to be characteristic of, most of the epizoic Loxosomatidae. For example, Nielsen (1966) describes *Loxosoma davenporti* as normally settling inside the tubes of the malidanid polychaete *Clymenella zonalis*, but as completely absent from the tubes of the closely related *Clymenella torquata*, which is found much more frequently than *Clymenella zonalis* on the same sandy bottoms. Consequently, many authors consider the host a sufficient species character for the identification of loxosomatids. But the host can only be employed as a reliable species character if its relationship with the loxosomatid is specific; *i.e.*, determined by a strict physiological dependence. A shared preference of the host and its epizoan for the same microenvironment, or some structural feature of the host that offers the epizoan an ideal complex of life conditions (*e.g.*, a combination of mechanical shelter and a water current supplying food and oxygen and removing detritus) are situations in which host specificity is not a reliable species character. A majority of the guest-host relations in the loxosomatids seem to be of this latter type.

Only three of the loxosomatids discussed above are known to show a preference for specific hosts independent of the respective localities: *Loxosomella varians* for nephthyid polychaetes, *Loxosomella antarctica* for the brittle star *Ophiurolepis gelida*, and *Loxosomella compressa* for errant polychaetes of the family Polynoidae. The latter two loxosomatids were very abundant at many locations. *Loxosomella antarctica* is found predominantly on silty bottoms, on the oral disk between the arms of *Ophiurolepis gelida*, never on other ophiurids abundant in the same place. If nutrients are abundant, it also builds up crowded aggregations on the aboral side of its host and laterally along its arms. At adequate sites, where *Ophiurolepis* is lacking or very rare, *Loxosomella antarctica* does not switch to another ophiurid, but rather to an aphroditid polychaete, *Laetmonice producta*. On this second host, it occupies exclusively the tips of the dorsalmost notopodial setae in the first segments as well as the posterior dozen body segments.

The large robust zooids of *Loxosomella antarctica* are quite resistant to mechanical lesions (*cf.* regeneration capacity), as well as low oxygen supply. As can be seen from their stomach contents, consisting mainly of detritus particles and some larger ciliates mixed with fine mineral material, they are sediment feeders. Their requirements

are for a nutrient-rich fine sediment and a solid settling substrate offering a certain protection against predators and against being buried irreversibly under sediments. So this species thrives on hosts like *Ophiurolepis* and *Laetmonice* which creep on, or dwell in, the upper sediment layer.

Loxosomella compressa on arctic and subarctic shelves as well as in antarctic waters was detected exclusively on polychaetes of the family Polynoidae, attached basally to the notopodial setae of their hosts. A more detailed analysis of the microhabitat of *L. compressa* reveals that the only polynoidan species infested by this epizoan guest are those with notopodial setae that are thick and short, not too densely arranged, and covered by the elytrae. This loxosomatid has only exceptionally been found on polynoids with bushy, thinner notopodial setae or with parapodia not covered by the elytrae. Usually only smaller species, up to 10 cm in length, or younger specimens of larger polynoids are chosen as hosts. In culture experiments, the newly detached buds also settled on diverse non-living substrates (*cf. p. #*) exposed to the current.

Loxosomella compressa is smaller and less resistant to mechanical injury and low oxygen supply than *L. antarctica*. As can be demonstrated by an examination of its stomach contents, its diet consists mainly of small algae; predominantly small pennate diatoms. Consequently, its delicate zooids can grow only in a microhabitat that offers shelter against predators as well as against mechanical injury, but which also exposes them to a continuous water current and provides enough space for optimal feeding positions. Such conditions are preferably offered by smaller polynoid polychaetes, not dwelling in the sediment, but creeping on the exposed surface of sponges and on erect bryozoan and hydroid colonies. Other habitats, offering comparable physical conditions, may also be chosen as a substrate by *L. antarctica* and *L. compressa*. But the small loxosomatids are not easily detected amidst the bulk of possible substrates in dredged material; presumably they are usually overlooked during sorting. But when the hosts were kept for a while in well aerated aquaria, the loxosomatids were also found on various other non-living substrates.

From these observations, one can speculate that the choice of settling substrate, at least for these loxosomatid species, is determined by the physical structure of the microhabitat and the supply of an appropriate diet, rather than by specific physiological properties of the host itself. Thus, although most loxosomatids have preferred hosts, these can only be regarded as weak species characters.

(4) The observed *bipolar occurrence* of *Loxosomella antedonis*, *L. compressa*, and *L. varians* in coastal waters suggests, at first glance, a discontinuous, exclusively *bipolar distribution* of these species. Their northern distribution in the litoral and sublitoral of the continental coasts stretches from Greenland (*L. antedonis*) and the Eurasian

polar shelf (*L. compressa* and *L. varians*), along the northern European coasts, south to about 54°N in the southeastern North Sea. In the South Atlantic and the Atlantic sector of the Antarctic Ocean, these three species are common from the Weddell Sea, and north to the Islas Malvinas and South Georgia (about 54°S). To date, none of them has been found along the eastern or western mid-Atlantic coasts, although the entoproctan fauna of the Central European shelf, in particular, as well as of the Caribbean, Argentinean and Chilean coasts have been well investigated. At present, however, nothing is known about the depth range of these species and their possible distribution along the Atlantic deep sea ridges.

Comparable examples of a suggested bipolar distribution of a single species are extremely rare and still controversial, the best known being the bipolar occurrence of *Priapulius caudatus* (Ekman, 1935; van der Land, 1970). A discontinuous distribution of taxa above the species level can be explained by the break-up of an originally continuous area of distribution by geomorphic events, such as continental drift, and long term climatic changes. At the species level, on the other hand, it seems unlikely that populations separated over geological periods could remain uniform in their specific characters unless at least a limited amount of genetic exchange were maintained between them.

But how can such an exchange take place in the present case? Under the conditions of an exclusively bipolar distribution, such a genetic exchange between the North and South Atlantic populations of the above loxosomatids must be excluded, because the life span of individual loxosomatid zooids does not exceed 4–6 weeks, and the mobile larval phase lasts scarcely more than 8 days.

Neither passive drifting with currents, nor transport by fast swimming hypothetical hosts such as whales could proceed quickly enough to maintain a sufficient exchange between populations of the North and South Atlantic. Nor can the considerable increase of the shipping traffic in the past decades be responsible for this distribution. One might postulate that the Antarctic faunal region had been colonized only recently by these species. But at least for *Loxosomella compressa* and *L. varians*, their distributions in both the Arctic and Antarctic regions were already established in the 19th century, as documented by the evaluation of several samples from the turn of the century (Franzén 1973; this paper).

Thus a recent *continuous distribution* by colonization along the Atlantic ridges, and possibly the deep sea basins, must be postulated as being responsible for the *bipolar occurrence* of these loxosomatids in shallow coastal waters. More deep sea samples should be obtained and evaluated so that this hypothesis can be tested.

As far as can be judged to date, the three loxosomatid species mentioned above are distributed in the Atlantic sector of the Antarctic Sea only, and they seem to be ab-

sent from the Pacific sector. The faunal connection between the North and South Atlantic must, therefore, be much more intense than the circum-Antarctic faunal migrations.

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